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AN OVERVIEW OF INVASIVE WOODY PLANTS IN THE TROPICS

TABLE OF CONTENTS

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SUMMARY

Using databases and associated literature a review of invasive woody plants in the tropics and sub-tropics is presented. It focuses on information not readily available in published overviews on biological invasions.

Using data on 3579 bibliographical references and 653 invasive woody species temporal, spatial, taxonomic and ecological trends and patterns are described. Data for the tropics and sub-tropics are compared to those of the world.

The importance of historical and socio-economic factors in the introduction and subsequent spread of exotic species is examined. The difficulty in identifying the taxonomic nature of an introduced plant, ascertaining whether a plant is native or alien and obtaining historical information is stressed.

Invasive tendencies of woody species and the predictability of a species becoming invasive are reviewed in relation to species characteristics, disturbance regimes and environmental factors. Time-lags between the introductions of tropical woody plants and their spread are investigated in more detail. Published evidence shows that major changes in a biotic factor (e.g. grazing, pollinator, seed disperser) or an abiotic (e.g. fire, wind, flood, logging) factor determines the duration of time-lag.

A list of 235 woody species in tropical and sub-tropical regions is presented with species listed according to life-form and degree of invasiveness. Eighteen species selected from the most highly invasive species category are investigated in greater detail in the form of short species accounts.

1. INTRODUCTION

Biological invasions are considered to be one of the major threats to the earth's biodiversity. Many animal and plant taxa are highly invasive and some species dramatically affect the structure and function of ecosystems. During the 1980s the Scientific Committee on Problems of the Environment (SCOPE) programme attempted to draw attention to this major threat as well and summarize the available information. As a result a large number of books and proceedings were published (e.g. Drake *et al.* 1989, Duffey 1988, Groves & Di Castri 1991, Ramakrishnan 1991). In the plant kingdom a great number of invasive species are woody. However, a perusal of the SCOPE-related literature indicates that no serious attempt was made at gathering, analyzing and interpreting the available information on woody plant invaders. For example, Rejmáneck (1989) in his review included only 32 woody species. Whitmore (1991) produced a similar review for the tropics, chiefly based on evidence from south-east Asia, and claimed that all tropical moist forests are resistant to invaders although several cases had been previously reported (Binggeli 1990). The books by Cronk & Fuller (1995), Pysek *et al*. (1995) and Rejmáneck (1996) provide a much broader, but not comprehensive, review of the subject.

In this study on woody plant invasions it is intended to:

1. Provide an overview of the literature and of the main taxonomic, biogeographical and ecological attributes of woody invasive plant species with special reference to the tropics and subtropics (including wet, dry and montane regions).

2. Investigate some historical aspects of woody species introductions in the tropics in some detail,

3. Raise some key ecological questions such as the existence of time-lags, the reasons for their existence, and whether we can predict events after a potential introduction,

4. Produce a provisional list of tropical invasive woody plants, and

5. Provide species accounts on a number of highly invasive species and which pay special attention to the autecology of the invaders. An attempt is made to evaluate differences in ecology between the native and invaded ranges in each of these accounts.

Much of the information reported in this study is based on a number of databases on invasive woody plants and associated reprint collection.

2 OVERVIEW OF INVASIVE WOODY PLANTS AND THEIR COMPARATIVE ANALYSIS

2.1 INTRODUCTION

In this section an overview of woody plant species with special reference to the tropics is presented using the information contained in two databases containing information on, respectively, bibliographical references and information on 653 woody species.

This is a preliminary overview, as data on a number of species and ecosystem attributes has yet to be entered in the database and many bibliographical references have yet to be traced. Wherever possible the data from the bibliographical database analyzed in 1994 (up to the year 1992) is compared with the 1998 analysis which includes data until the year 1996. During that period the data set of the bibliographical reference database has roughly doubled.

2.2 BACKGROUND

A rapid perusal of the literature indicates that there are hundreds, even thousands, of invasive plant species worldwide. In the plant kingdom a large proportion of invasive species is woody (including sub-shrubs with stems woody at the base). However, it is difficult to gain an overall picture of woody plant invasions because of the limited number of well studied cases and the difficulty in tracing published information on biological invasions. Therefore, only a long-term project can provide the basis to an overview of invasive woody plants. In order to do so, it is essential to gather information on any species exhibiting an invasive tendency as well as information on the biology and ecology of each plant and ecological and environmental information on the native and invaded ranges. This information gathering was initiated in the mid 1980s. To summarize and analyze some of the information gathered a relational database was set up. The Invasive Woody Species Database (using R:Base run on a PC-compatible 486 notebook) was set up between 1990 and 1993 and is based on information gathered over 10 years of literature search. A bibliographical reference database was initiated in 1990 and data entered thereafter. In 1993 a relational database on invasive woody plants was set up and includes a number of species (e.g. life-form, life cycle...) and invaded ecosystem attributes.

For practical reasons, mainly as a result of how data was initially entered into the database, sub-tropical areas (up to a latitude 30^{o}) only include Florida, the Indian peninsula, Pacific islands, Northern Africa, South America, but fail to include southern Africa and parts of sub-tropical Australia.

2.3 INVASIVE WOODY SPECIES DATABASE

2.3.1 DATABASE STRUCTURE AND CONTENT

The Invasive Woody Species Database (due to lack of computer power) is in two main parts which can easily be connected: the bibliographical reference database (Reference Database) and the invasive plant database (Species Database). The Reference Database is composed of standard fields and contains over 18500 references of which about 6000 pertain to invasive organisms and the majority of the others contain ecological information relevant either to the autecology of these invasive organisms and or the ecology of the native and invaded ecosystems. In this study the term invasive is defined as the establishment of self-regenerating, usually expanding, populations of an introduced species in a free-living state in the wild (Binggeli 1994) and is somewhat different from that of Cronk & Fuller (1995) who do not include species invading man-made habitats. Pysek (1995) reviewed the terminology associated with invasive plants. Each reference record has a number code and a field containing a large number of key words (based on the text rather than the title or the abstract) including species names, geographic areas and life form. The Species Database is relational and consists of four tables, two of which contain information on respectively 42 species attributes and 10 ecosystem attributes. All information entered in the Species Database is linked to a reference in the Reference Database using a number code (where possible a copy of the original publication has been kept in files organised by genera or region). Since the quality and the quantity of the available information are often poor, the various attributes included in the Species Database were necessarily chosen according to the availability of information rather than their importance in generating hypotheses or making predictions.

The great majority of biological information is not discrete. To simplify the database much of the information was categorized, often subjectively (for instance life-forms: tree vs shrub; degree of invasiveness). Some of the results presented below may not represent distinct guilds but may prove be part of a continuum when more data has been added.

It is intended to continue refining and expanding the species database. This will result in the inclusion of new attributes and possibly the rejection of some existing ones.

2.3.2 DATASET INCLUDED IN PRESENT ANALYSIS

2.3.2.1 Reference Database

Bibliographic references entered into the Reference Database have been obtained by scanning Forestry Abstracts, Current Advances in Botanical Sciences, journals' table of contents, floras and bibliographies of a large number of published papers. Any publication which reported the natural regeneration of a woody species outside its natural range was included in the database regardless of its degree of invasiveness or invaded habitats. In order to reduce some degree of bias all references dealing with three species investigated in detail by the author were not included. They are *Acer pseudoplatanus* L. (184 records), *Hippophae rhamnoides* L. (25 records) and *Maesopsis eminii* Engl. (33 records). The total number of references included in the present analysis is 3579, of which notes on or reprints of around 1000 publications are with P.B. Searching has been completed to the end of 1996 as many publications post 1996 publications have yet to be traced and entered. For the 1992 dataset searching had been carried out until late 1994 and includes 1924 records.

2.3.2.2 Species database

Published information pertaining to invasive woody plants is often subjective and difficult to interpret. For the purpose of this study, data for a number of attributes (e.g. degree of invasiveness, purpose of introduction and habitat types) have been amalgamated into a small number of broad categories. Wherever possible, invasive events are scored as possibly/potentially, moderately or highly invasive. Introduced species recorded as possibly/potentially invasive are locally regenerating but the extent of spread is not known or is limited. Moderately invasive species are spreading but still occur at low densities and are not considered an immediate problem. Highly invasive species have become dominant or co-dominant in the invaded region and are considered a threat to the native flora and ecosystem. These species are usually subjected to some form of control. Out of 1198 invasive events it has been possible to assess the degree of invasiveness in 1060 cases.

Throughout, the data are presented in relation to the degree of invasiveness. As each species can be invasive in more than one region with differing degrees of invasiveness, the highest degree of invasiveness is used for each species in the presentation of the data dealing with species attributes. Results are presented for attributes where data are currently (1/3/1998) available for at least 30% of the species.

2.4 RESULTS AND DISCUSSION

2.4.1 Reference database

Temple (1990) remarked that he was amazed that so few papers on exotic organisms were published in Conservation Biology, suggesting a lack of research in this important field of conservation. In fact, the number of references relating to woody invasive plants has steadily increased since the last century with the 1987-1996 period representing nearly half of the total (Table 2.1). The growth in published material on invasive woody plants, both worldwide and in the tropics, exhibit an increase similar to that of publications on African moist forests but compares favourably with the trend for sycamore (*Acer pseudoplatanus*) (Table 2.1). However, the rate of increase in the number of publications on invasive woody plants appears to have levelled off since 1990 and just over 200 publications have appeared yearly. The three data sets show the same levelling off or even decrease in publication rate associated with the World War II period.

It is estimated that around 80-90% of all references published on sycamore, with the exception of those pertaining to suspension cell cultures, have been traced, but out of 2958 references only 30% and 17% are available from, respectively, Forestry Abstracts and Biological Abstracts searches. This clearly indicates that on-line databases only provide a starting point to a thorough literature search. It is estimated that the 3579 references represent no more than about half of all published material on invasive woody plants, although it does probably include the greater majority of key publications.

Table 2.1. Comparative increase in the number of references relating to woody invasive species worldwide and the tropics/sub-tropics, African moist forests and sycamore, *Acer pseudoplatanus* (data expressed as a %)

	Woody invasions		African	sycamore
	world	tropics	forests	
N	3579	1312	1137	2958
year				
>1896	0.7	0.6	0.3	5.4
1896-01	0.1	0.1	0.7	1.2
1902-06	0.2	0.2	0.6	1.1
1907-11	0.2	0.2	0.7	1.6
1912-16	0.3	0.4	0.2	1.2
1917-21	0.3	0.3	0.1	0.7
1922-26	0.6	0.5	0.6	1.0
1927-31	0.8	1.1	0.7	1.7
1932-36	0.9	1.0	1.7	1.5
1937-41	0.8	1.0	1.4	1.2
1942-46	0.8	1.1	0.5	1.0
1947-51	1.5	1.7	3.0	2.4
1952-56	2.5	1.9	3.2	5.3
1957-61	2.2	2.0	4.4	4.6
1962-66	3.7	3.6	4.0	4.2
1967-71	4.7	4.4	5.4	8.0
1972-76	6.9	5.9	5.5	10.0
1977-81	8.9	7.2	7.8	11.0
1982-86	15.0	13.5	10.1	11.0
1987-91	22.7	24.6	24.6	14.9
1992-96	26.2	28.7	24.5	11.6

Out of the 3579 references on invasive woody plants, very few (ca <5%) report case histories of biological invasions. The majority mention invasiveness only in passing or in a very descriptive manner. A large number of publications (Table 2.2) are review papers (12.5%) and there was a strong increase in their relative importance during the late 1980s, chiefly as a result of the SCOPE publications. In the 1990s the proportion of review papers still appears to be increasing. Papers on biological control and other forms of control represented respectively 11.5% and 16.6% of the total (note that some references classified under biological control also refer to other means of control). The proportion of publications relating to biological control, in both the world and the tropics, has gone through cycles with peaks around 1950, the late 1970s and 1990s whereas comparatively few publications on biological control appeared in the 1950s and around 1980. Prior to 1976 the proportion of biological publications was much higher in the tropics than worldwide, but since the late 1970s a similar proportion has been published (Table 2.2).

Table 2.2. Changes in the relative importance of review papers and publications on biological control relating to woody invasive species worldwide and in the tropics/sub-tropics.

	all references		general and review references		biological control references	
	world	tropics	world	tropics	world	tropics
N	3579	1312	446	171	410	215
%	100	100	12.5	13.0	11.5	15.6
year	N	N	%	%	%	%
< 1896	26	7	7.7	-	-	-
1897-01	2	1	-	-	-	-
1902-06	6	3	-	-	16.6	33.3
1907-11	8	3	-	-	-	-
1912-16	11	5	9.1	-	-	-
1917-21	12	4	16.7	-	8.3	-
1922-26	21	6	4.8	-	4.8	16.7
1927-31	28	14	7.1	7.1	14.3	7.1
1932-36	31	13	3.2	-	9.7	23.1
1937-41	29	13	13.8	7.7	10.3	23.1
1942-46	28	14	7.1	7.1	7.1	14.3
1947-51	57	22	-	-	5.3	13.6
1952-56	91	25	6.6	8.0	6.6	24.0
1957-61	79	27	7.6	7.4	13.9	25.9
1962-66	132	48	9.1	12.5	12.1	22.9
1967-71	170	58	7.1	6.9	12.3	24.1
1972-76	248	77	5.2	3.9	6.0	10.4
1977-81	319	94	8.8	11.7	8.8	11.7
1982-86	535	177	9.5	7.3	10.5	13.0
1987-91	813	324	16.4	15.7	13.8	16.0
1992-96	936	376	18.2	20.2	13.6	17.8

The biogeographical origin of the references is in decreasing order of importance from North America, Australia, South Africa, New Zealand, British Isles, Hawaii and tropical Africa (Table 2.3). It is followed by Germany, which in the English-speaking world, is not regarded as a region susceptible to woody species invasions and/or considered to be interested in the phenomenon (Germans scientists were not involved in the SCOPE programme). A comparison of the data for 1992 and 1996 indicate that there has been a relative decrease in the number of publications produced in South Africa and New Zealand.

It is worth noting that all the regions with the highest number of references are historically linked with Britain and it is not clear whether this is due to the historical factors such as interest in natural history (chiefly perception of nature) and/or horticultural interest and/or language barriers, or reflect the worldwide pattern and severity of woody invasions. The number of references relating to islands was 1276 (617 in the tropics) and to the tropics was 1312, including 137 for tropical Africa and 140 for Florida. The relative proportion of the figures for 1992 and 1996 are broadly similar.

Table 2.3. Geographical focus of bibliographical references (regions with more than 100 records in 1996 included).

Region		Year	
		1996	1992
North America (except Florida)		547	272
Australia		495	202
South Africa		389	248
Hawaii		318	148
British Isles		316	169
New Zealand		309	206
Pacific (other than Hawaii)		224	87
Florida		140	45
Tropical Africa		137	78
Germany		116	59
Islands	-world	1276	659
	-tropics	617	295
World		3579	1924
Tropics		1312	610

Table 2.4 gives the number of publications in which a genus is given as invasive and includes genera with more than 70 and 20 records in respectively the world and the tropics/sub-tropics. Genera with more than 150 records include two genera each with only one invasive species (*Ulex* and *Lantana*) and four with several species (*Acacia*, *Pinus*, *Psidium* and *Rubus*). Some genera are reported in a large number of publications either in the tropics/sub-tropics (e.g. *Psidium*, *Melaleuca* and *Chromolaena*) or temperate zone (e.g. *Pinus*, *Rubus* and *Hakea*) while others are widely reported in both (*Lantana*, *Acacia* and *Ulex*). Between 1992 and 1996 the number of publications for some genera has increased much faster (e.g. *Psidium* and *Miconia*) or much slower (e.g. *Ulex*) than for the majority of genera. The rapid increase in the number of publications on *Miconia* and *Cryptostegia* reflects the rather recent realisation of their invasive potential and impact on native vegetation.

Table 2.4. Genera referred to in the largest number of publications.

WORLD			TROPICS AND SUB-TROPICS		
Genera	Year		Genera	Year	
	1996	1992		1996	1992
Lantana	286	137	*Lantana*	225	100
Acacia	263	189	*Psidium*	189	83
Ulex	207	155	*Mimosa*	132	45
Psidium	194	83	*Chromolaena*	108	53
Rubus	183	113	*Melaleuca*	106	64
Pinus	172	124	*Schinus*	78	49
Lonicera	138	64	*Acacia*	75	34
Mimosa	134	45	*Passiflora*	72	48
Chromolaena	127	80	*Myrica*	70	36
Tamarix	124	61	*Clidemia*	65	32
Melaleuca	106	64	*Rubus*	61	40
Rhododendron	106	54	*Cryptostegia*	34	3
Hakea	101	67	*Ulex*	34	20
Schinus	96	59	*Miconia*	28	4
Robinia	92	60			
Passiflora	79	51			

The difficulty in gaining information is illustrated in Table 2.5, where the journal, which published the largest number of papers on invasive woody plants, is noted to contain only 1.2% of the total number of references. Books, including floras and reports, account for 14.1% of the total while chapters in books and conference proceedings represent 19.3% of the total. For the tropics/sub-tropics alone the figures are markedly similar but journals publishing the largest proportion of papers is different. Since 1992 new publications have appeared and others have tended to publish fewer articles on invasive woody plants.

Table 2.5. Sources of bibliographical references (figures in brackets are %).

WORLD			TROPICS AND SUB-TROPICS		
Year	1996	1992		1996	1992
Total	3579	1924		1312	610
%	(100)	(100)		(100)	(100)
Books (including floras & reports)	506 (14.1)	264 (13.7)	Books (including floras & reports)	201 (15.3)	90 (14.8)
Chapters in books & conference proceedings	689 (19.3)	423 (22.0)	Chapters in books & conference proceedings	289 (22.0)	141 (23.1)
Journals, bulletins & magazines	2384 (66.6)	1237 (64.3)	Journals, bulletins & magazines	822 (62.7)	379 (62.1)
Main Journals					
N.Z. J. Bot.	42	22	Pac. Sci.	27	10
Biol. Conserv.	40	24	Biol. Conserv.	16	13
BSBI News	31	17	Proc. Hawn entomol. Soc.	15	14
Pl. Prot. Quart.	31	6	Monogr. Syst. Bot. MO Bot. Gard.	14	11
US Dept Agric., Agric. Handb.	31	28	Newsl. Hawn bot. Soc.	14	2
Pac. Sci.	27	11	Aliens	13	0
Ecology	26	11	Agnote	11	11
J. Ecol.	26	21	Atoll Res. Bull.	11	1
J. appl. Ecol.	24	14	Pl. Prot. Quart.	11	3
Aliens	21	0	Qld Agric. J.	11	4
S. Afr. J. Bot.	20	17	Entomophaga	10	3
Agric. Ecosyst. Environ.	23	16	Ind. Forester	10	8
S. Afr. For. J.	18	16	Agric. J. (Fiji)	9	6
S. Afr. J. Sci.	16	15	J. Biogeogr.	8	7

The majority of publications relating to invasive woody plants are either not abstracted or make no reference to invasive woody plants in the title, abstract or key words, again highlighting at the difficulty in gathering information. The high ranking of, for instance, BSBI News (not abstracted) in Table 2.5 points out that much of the available information is anecdotal and often collected by amateur botanists. As a result the quantity of information available for a particular species can be very limited. Some genera are widely used in review papers as typical examples of invasive woody plants and some of the species may have be cited in a high proportion of review papers, and this is particularly the case of *Myrica* and *Melaleuca* with respectively and third and a quarter of their publications.

Some of the changes observed between the 1992 and 1996 datasets are undoubtedly due to changes in publication rates in various countries, genera and journal/magazine/bulletin, however some of the variation is also due to literature hitherto unavailable or not scanned.

2.4.2 Species database

2.4.2.1 Taxonomy

Worldwide 653 woody plant species, belonging to 315 genera and 110 families, have been recorded as being invasive. The Rosaceae and legume families, and to a lesser extent the Pinaceae and Myrtaceae, contain a large number of invasive woody plants (Table 2.6). However most species of the Rosaceae are possibly/potentially or moderately invasive and relatively fewer are highly invasive. On the other hand families such as the Asteraceae, Myrtaceae and Melastomaceae have a number of highly invasive species but few possibly/potentially invasive species and are chiefly tropical/sub-tropical species. Regardless of the degree of invasiveness the Mimosaceae contains the largest number of invasive species in the tropics.

Table 2.6. Families with highest number of invasive woody species (Degree of invasiveness (DI): 1 = possibly/potentially invasive, 2 = moderately invasive, 3 = highly invasive, N = no. of species).

WORLD

Total		DI 1		DI 2		DI 3	
Family	N	Family	N	Family	N	Family	N
Rosaceae	98	Rosaceae	34	Rosaceae	50	Mimosaceae	17
Mimosaceae	49	Papilionaceae	12	Mimosaceae	21	Rosaceae	14
Papilionaceae	27	Mimosaceae	11	Myrtaceae	13	Asteraceae	7
Pinaceae	27	Pinaceae	8	Pinaceae	12	Pinaceae	7
Caesalpiniaceae	21	Salicaceae	7	Caesalpiniaceae	11	Myrtaceae	6
Myrtaceae	20	Caesalpiniaceae	7	Ericaceae	11	Papilionaceae	5
Asteraceae	17	Caprifoliaceae	6	Oleaceae	11	Caprifoliaceae	4
Ericaceae	17	Berberidacea	5	Solanaceae	11	Melastomaceae	4
Oleaceae	17	Cornaceae	4	Papilionaceae	10	Solanaceae	4

TROPICS AND SUB-TROPICS

Total		DI 1		DI 2		DI 3	
Family	N	Family	N	Family	N	Family	N
Mimosaceae	31	Mimosaceae	4	Mimosaceae	15	Mimosaceae	12
Myrtaceae	14	Caesalpiniaceae	3	Rutaceae	9	Myrtaceae	5
Caesalpiniaceae	13	Papilionaceae	3	Caesalpiniaceae	8	Asteraceae	4
Rosaceae	11	Acanthaceae	2	Myrtaceae	8	Melastomaceae	4
Rutaceae	10	Myrsinaceae	2	Euphorbiaceae	6	Rosaceae	4

2.4.2.2 Biogeography

In the temperate zone a large number of invasions have been reported from most regions with the exception of Southern America and Asia (Table 2.7). In the tropical zone most invasions are reported from Pacific and Indian Ocean islands, with no records from the Amazon region! Worldwide the same number of invasions of continents and oceanic islands has been reported (Table 2.8). When one takes the degree of invasiveness into account the ratio between possibly/potentially, moderately and highly invasive species is similar on continents and islands (Table 2.8). However, there are relatively few highly invasive woody species on islands situated on continental shelves (e.g. British Isles) than isolated ones (e.g. Hawaii). In the tropics there are relatively fewer invasive species on continents and on continental shelf islands. The relative importance of possibly/potentially invasive species is much lower in tropical regions than for the world but this is probably due to under-recording.

Table 2.7. Biogeographical distributions of invasive events (DI as in Table 2.6, DI available for 1060 invasive events, N = no. of species).

	Total	DI1	DI2	DI3
Region	N	N	N	N
Europe	250	107	122	21
Pacific Islands	155	31	83	41
North America	143	37	82	24
New Zealand	134	43	78	13
Australia	88	35	33	15
Indian Ocean Islands	74	9	50	15
Southern Africa	62	13	29	20
Tropical Africa	57	13	32	12
Asia	42	7	22	13
Southern America	27	4	18	5
West Indies	12	1	10	1
Atlantic Islands	11	3	8	-
Madagascar	8	-	4	4
Others	2	-	2	-

Table 2.8. Relative incidence of invasions on continents and oceanic islands (DI as in Table 2.6, DI available for 1060 invasive events, N = no. of invasive events).

	WORLD				TROPICS AND SUB-TROPICS			
		DI 1	DI 2	DI 3		DI 1	DI 2	DI 3
	N	%	%	%	N	%	%	%
Continents	529	30	52	18	133	23	56	21
Oceanic islands	531	27	56	17	260	16	60	24
Oceanic islands								
isolated	396	22	58	20	247	16	60	24
continental shelf	135	41	50	9	13	15	70	15

2.4.2.3 Ecology

Species attributes

Shrubs (height < 5 m) are the commonest invasive life-form followed by small trees (height 5-15 m) and trees (height > 15 m). The relative importance of shrub species is much greater among potentially invasive species than in the other two categories (Table 2.9). There are few invasive woody climbers. In tropical regions the relative importance of possibly/potentially and moderately invasive shrubs is much lower.

Table 2.9. Life-forms of invasive woody species (DI as in Table 2.6, N = no. of species).

WORLD

	Height	Total		DI 1		DI 2		DI 3	
		N	%	N	%	N	%	N	%
Trees	>15m	166	25	34	20	102	28	30	25
Small trees	5-15m	181	28	32	18	115	32	34	29
Shrubs	< 5m	264	41	97	56	125	35	42	35
Climbers		42	6	11	6	18	5	13	11

TROPICS AND SUB-TROPICS

	Height	Total		DI 1		DI 2		DI 3	
		N	%	N	%	N	%	N	%
Trees	>15m	73	30	7	23	51	34	15	24
Small trees	5-15m	90	36	11	35	62	41	17	27
Shrubs	<5m	63	26	10	32	29	19	24	38
Climbers		19	8	3	10	9	6	7	11

The relative proportions of evergreen and thorny species increase with the degree of invasiveness, although overall the total number of thorny species is low (Table 2.10). The majority of tropical species are evergreen. Wind-pollination is commoner in possibly/potentially invasive species and insect-pollination more frequent in moderately and highly invasive species and in the tropics the relative importance of wind-pollination increases with the degree of invasiveness (Table 2.10). Some moderately and highly invasive species are amphophilous, bird-pollinated or self-pollinated. A variety of fruit types characterize invasive woody plants including, in decreasing degree of importance, berries, pods, capsules, drupes and cones. Birds are the main dispersal agent followed by wind. The relative importance of wind-dispersed species decreases with the degree of invasiveness (Table 2.10). The relative proportions of fruit types and dispersal agents of tropical species are similar to that of the world, although some fruit types are not represented among the tropical examples.

In the majority of species, fruit size (to the nearest cm) was 1 cm and 3cm with greater variation among pods (1-60 cm) than among other fruit types (1-15 cm). Most fruits contained one or two seeds, but a few had a larger number (up to a thousand). The size of most seeds was between 1 mm and 6 mm with a few reaching 50 mm.

Table 2.10. Various species attributes characterising invasive woody plants (DI as in Table 2.6, in brackets sample size, N = no. of species).

	WORLD						TROPICS AND SUB-TROPICS					
	DI1		DI2		DI 3		DI 1		DI 2		DI 3	
	N	%	N	%	N	%	N	%	N	%	N	%
Deciduousness	(383)						(112)					
deciduous	58	57	100	47	27	39	2	18	22	30	3	11
evergreen	36	35	100	47	35	51	7	64	46	63	20	71
semi-evergreen	8	8	12	6	7	10	2	18	5	7	5	18
Thorniness	(220)						(110)					
thornless	36	97	114	90	41	73	8	88	62	86	26	70
thorny	1	3	13	10	15	27	1	12	10	14	11	30
Pollinating agent	(161)						(61)					
amphophilous	-		-		3	7	-		-		1	5
bird	-		1	1	1	2	-		-		-	
insect	11	38	57	63	22	54	4	100	32	86	12	60
wind	18	62	32	35	14	35	-		4	11	6	30
self-pollinated	-		1	1	1	2	-		1	3	1	5
Fruit type	(520)						(188)					
achene	2	1	11	4	7	7	-		4	4	3	6
berry	32	23	59	21	27	27	4	16	21	19	12	23
capsule	20	15	55	19	19	19	5	20	24	21	11	21
catkin	8	6	8	3	1	1	-		-		-	
cone	10	7	18	6	9	9	-		3	3	3	6
drupe	17	13	63	22	11	11	7	28	30	27	8	15
follicle	10	7	13	5	1	1	-		3	3	-	
nut	2	1	6	2	-		-		-		-	
pod	26	19	37	13	23	23	9	36	23	20	15	29
pome	7	5	7	2	1	1	-		1	1	-	
samara	4	3	9	3	1	1	-		2	2	-	
Dispersal agent	(287)						(117)					
mammal	2	3	9	6	4	5	-		3	5	4	10
bird	29	49	71	46	38	49	5	62	27	46	17	43
explosive	-		1	1	3	4	1	13	1	2	2	5
insect	-		-	2	3				-		2	5
mammal	-		3	3	5	6	-		2	3	4	10
water	1	2	2	1	3	4	-		2	3	3	7
wind	27	46	65	43	22	29	2	25	24	41	8	20

The purpose of introduction of species which have become invasive is not known for a large number of invasive events. Introductions for amenity purposes, and to a lesser extent for forestry and agricultural purposes, have been responsible for most reported cases of invasions (Table 2.11). Agricultural introductions result in relatively fewer cases of highly invasive species whereas the reverse is true for forestry introductions. In the tropics the relative proportion of introductions for agricultural, botanical and forestry purposes is greater, however this trend is not observable in highly invasive species rather than amenity purposes.

Table 2.11. Main purpose of introductions (DI as in Table 2.6, N = no. of invasive events).

WORLD

	DI1		DI2		DI3		Total	
	N	%	N	%	N	%	N	%
Agriculture	37	3.5	67	6.3	16	1.5	120	11.3
Botanic gardens	3	0.3	11	1.0	6	0.6	20	1.9
Forestry	27	2.5	70	6.6	34	3.2	131	12.3
Amenity	114	10.8	164	15.5	49	4.6	327	30.9
Landscape	7	0.7	11	1.0	6	0.6	24	2.3
Accidental	1	0.1	-		1	0.1	2	0.2
Unknown	114	10.7	250	23.6	72	6.8	436	41.1
Total	303	28.6	573	54.0	184	16.4	1060	100.0

TROPICS AND SUB-TROPICS

	DI1		DI2		DI3		Total	
	N	%	N	%	N	%	N	%
Agriculture	22	5.6	43	10.9	9	2.3	74	18.8
Botanic gardens	3	0.8	9	2.3	4	1.0	16	4.1
Forestry	4	1.0	38	9.7	13	3.3	55	14.0
Amenity	16	4.1	42	10.7	23	5.8	81	20.6
Landscape	-		3	0.8	4	1.0	7	1.8
Accidental	1	0.2	-		1	0.2	2	0.4
Unknown	27	6.9	96	24.4	35	9.0	158	40.3
Total	73	18.6	231	58.8	89	22.6	393	100.0

Ecosystem attributes

In only half of the reported invasive events is it possible to determine the invaded habitat (Table 2.12). Most invasions occur in forests - both natural and disturbed. The majority of invaded habitats are highly disturbed and in most instances this has resulted from human disturbance. Forests appear to be the natural habitats most susceptible to invasions by woody plants. Results for tropical regions do not differ markedly from world trends.

Table 2.12. Habitat types invaded by invasive woody plants (DI as in Table 2.6, N = no. of invasive events).

WORLD

		DI 1		DI 2		DI 3		Total	
		N	%	N	%	N	%	N	%
Disturbed grounds		35	3.3	71	6.7	36	3.4	142	13.4
Forests	-natural	10	0.9	30	2.8	19	1.8	59	5.5
	-disturbed	26	2.4	82	7.7	40	3.8	148	13.9
	-plantation	4	0.4	7	0.7	3	0.3	14	1.4
Hedges		2	0.2	5	0.5	1	0.1	8	0.8
Grasslands		12	1.1	23	2.1	18	1.7	53	4.9
Riverbanks		9	0.9	23	2.1	10	0.9	42	3.9
Roadsides		11	1.0	23	2.1	3	0.3	37	3.4
Swamps		4	0.4	4	0.4	2	0.2	10	1.0
Dunes		5	0.5	8	0.8	3	0.3	16	1.6
Bogs/heathland/fynbos		1	0.1	9	0.9	7	0.7	17	1.7
Cliffs		3	0.3	5	0.5	-	0	8	0.8
Unknown		181	17.1	283	26.7	42	3.9	506	47.7
Total		303	28.6	573	54.0	184	17.4	1060	100.0

TROPICS AND SUB-TROPICS

		DI1		DI2		DI3		Total	
		N	%	N	%	N	%	N	%
Disturbedgrounds		12	3.0	25	6.4	21	5.3	58	14.7
Forests	-natural	7	1.8	17	4.3	13	3.3	37	9.4
	-disturbed	9	2.3	45	11.4	15	3.8	69	17.5
	-plantation	1	0.3	4	1.0	3	0.7	8	2.0
Hedges		-		-		-		-	
Grasslands		2	0.5	8	2.1	10	2.5	20	5.1
Riverbanks		-		-		2	0.5	2	0.5
Roadsides		1	0.3	5	1.2	-		6	1.5
Swamps		1	0.3	1	0.3	2	0.5	4	1.1
Dunes		1	0.3	1	0.3	1	0.3	3	0.9
Bogs/heathland/fynbos		-		-		-		-	
Cliffs		-		-		-		-	
Unknown		39	9.8	125	31.8	22	5.7	186	47.3
Total		73	18.6	231	58.8	89	22.6	393	100.0

2.5 FUTURE PROSPECTS

2.5.1 CURRENT AND FUTURE PROBLEMS

When this invasive woody database was set up it was clear that many problems would arise. Some were predicted. Others have arisen since. Many of the difficulties are linked with our perceptions of nature and difficulties in communicating information. The main problems are:

1. The literature is very scattered.

2. Much more information is available than is currently held in the database.

3. Taxonomic difficulties, including hybridization, are major hurdles for many genera and since this is well-known the reader is referred to other literature for details (e.g. Stirton 1979, Swarbrick 1986).

4. Invasive hot spots have been clearly identified but have yet to be explained. In the literature on biological invasions historical, cultural, social and economic factors associated with humans have received little attention. Do invasive hot spots result from:

    a. cultural bias in recording,

    b. high levels of species introductions or,

    c. ecosystem susceptibility to invasions?

    or a mixture of these and other ecological factors. Above it has been pointed out that most cases of invasions have been reported by, and focus on, countries historically linked with Britain. Therefore, a cultural bias should not be underestimated.

5. Few species and ecosystem attributes have been looked at in any detail. Basic information such as life-history traits (e.g. pollinating agent, seed dispersal) are rarely reported even in case studies. Such information may often be obtained from other sources. A check list of attributes to be answered by workers in the field should be considered, which would provide us with a standardized set of data.

6. The status of some species is unclear, are they biological invasions or the result of natural dispersal? (see section 2 for details)

7. The families with the highest numbers of invasive woody species are given in Table 2.6. However, the invasive potential of a family can only be determined when the ratio of invasive species to the total number of woody species in a particular genera is known.

8. As in all literature based investigations, at least 95% of the data is secondary, dealing with species and habitats unfamiliar to the compiler.

2.5.2 DATABASE USE

In addition to the overview of invasive woody plants, the database has two main objectives:

To have an easily retrievable source of information on a particular species, including publications relating to it, and information on a number of species and invaded ecosystem attributes, and

to use the information to predict the invasive potential of a species in a particular habitat and/or region.

For predictive purposes invasive species must be compared with non-invasive species and with a sub-set of local floras for which the same type of information will need to be gathered. Ideally these non-invasive species should be chosen at random, but since information on them will be hard to obtain or unavailable, for present purposes well-documented species will be selected.

Invasive woody plants are a minor component of biological invasions. The time, financial resources and effort involved in producing this database, as well as what is still required to make it reasonably comprehensive, indicate that much needs to be done before an overall picture of biological invasions emerges.

3 INVASIVE WOODY PLANTS IN THE TROPICS

This section collates and summarizes relevant information not readily available elsewhere for an illustrative set of tropical species. Several major publications on invasive species have appeared in recent years (e.g. Drake *et al*. 1989, Ramakrishnan 1991, Cronk & Fuller 1995, Pysek *et al*. 1995, Carey *et al*. 1996, Sandlund *et al*. 1996, Williamson 1996). However there is need for a focus using, for each species, a set of headings covering life cycle attributes, consequences of invasive behaviour and integration into the invaded vegetation. Eighteen accounts are presented here on this basis. As a broader context four issues are discussed below. The first is the historical perspective. The second issue is how this relates to human aspirations, perceptions and actions. The biological basis of the contrast between extremely widely planted species apparently with no or minimal invasive tendencies and others which rapidly become problematic is the third issue. The final issue is possible future trends.

3.1 AN HISTORICAL PERSPECTIVE TO THE INTRODUCTION OF EXOTICS

Numerous woody species have been moved around the world, but the timing and the purpose of introductions, the species involved is poorly known. What remain of these introductions are agricultural, horticultural and forestry crops as well as invasive woody plants. Nevertheless, Spongberg (1990) has provided such an overview for North America. For most tropical regions such information has yet to be presented - but see Harris (1962) for the Leeward Islands, Duffey (1964) for Ascencion, Corlett (1992) for Hong Kong and Singapore, and Strahm (1993) - even though a foundation was laid long ago in the work of de Candolle (1860). Subsequently, Guppy (1917), Ridley (1930) and Sauer (1988) made significant advances in information collation and review where seed dispersal and plant migration are concerned. Crosby (1986) has related the pattern of introduction of plants, but particularly herbaceous agricultural weeds, to the European conquest of the world. A conspicuous omission from the studies carried out in the past has been the African situation. In this brief review we have therefore included a preliminary review for tropical Africa.

For the purpose of woody plant introductions into tropical Africa four main phases may be recognized:

- early exploration and slave trade,
- early colonial period,
- colonial exploitation, and
- post colonial development

Early exploration and slave trade

Europeans first settled in the Gulf of Guinea in the late 15th century. By the 18th century a number of French and English forts were scattered along the Golden Coast. These forts were involved in the slave trade and each of them had a gardens in which a number of crops, including many tropical American and Asian fruit trees, were grown (Juhé-Beaulaton 1994). These included *Anacardium occidentale*, *Citrus* spp. and *Psidium guajava*. A number of weeds were accidentally introduced when American crops were brought to Africa (Wild 1968).

Early colonial period

In Tanzania, non-indigenous plants were introduced to the experimental gardens of the Bagamoyo Mission shortly after its inception in 1869. From 1893 273 species of mostly tropical plants, including many ornamental and forest trees, such as *Acacia* spp., *Cinchona* spp., *Delonix regia*, *Eucalyptus* spp. and *Terminalia catappa*, were tested in an experimental nursery at Dar es Salaam which functioned as a seed production and distribution centre. Large quantities of seeds of various timber species were distributed to private planters and government stations. By 1903 a total of 118 indigenous and exotic timber species were under cultivation in the Lushoto District (Schabel 1990). Following the closure of the Kwai Agricultural Station, founded in 1896, a station was established in the East Usambaras at Amani in 1902 as an experimental site for field testing of exotic species (Iversen 1991). It included a botanic garden of ca 750 acres, including ca 500 acres of plantations, spreading between 400 and 1100 m (Fernie 1948). Nearly all species were introduced from other continents because they were either potential cash crops or known to be fast growing and useful in reforestation of steep mountain sites. Although the Amani forests contain several quality hardwood species, the research station was built with timber imported from Germany - it was cheaper to do that than to utilise local woods (Joelson 1928). Ornamentals, including temperate species, were introduced and it was the Director's (Prof. A. Zimmerman) hobby to collect plants from all over the world and try them out at Amani (Joelson 1928). Amani became a major distribution centre for seeds and seedlings in Tanzania and the tropics (Anon 1930, Schabel 1990).

Other botanical and experimental gardens in Africa were established from about 1890 including in Cameroon (Limbe, formerly Victoria, 1891) by the Germans, in Guinea (Fouta-Djalon) by the French, in Zaire (Eala) by the Belgium and in Lagos (1887) and Calabar (1893), both in Nigeria and Uganda (Entebbe, 1898) by the British.

Colonial exploitation

Soon after World War II a number of large-scale forestry plantations were established in order to enhance timber production. These plantations consisted of introduced species including *Eucalyptus* spp., *Gmelina arborea*, *Maesopsis eminii* and various conifers, especially *Cupressus* and *Pinus*. A number of agricultural crops were widely planted.

Post colonial development

In the last 20 years an increasing diversity of non-indigenous germplasm has been introduced to Africa as it has been to other tropical regions (Hughes 1994). Hughes documents in some detail the increase in the trade including increases in the number of species and provenances distributed as well as the number of planting locations.

In other parts of the tropics similar patterns of species introductions, particularly in relation to crop plants, forestry and ornamental woody species, have occurred. Tropical botanical gardens were set up in more places around the tropics, including several small oceanic islands (Pamplemouses, Mauritius; St Vincent, Caribbean), Asia (Bogor, Indonesia; Calcutta, India; Peradeniya, Sri Lanka; Singapore), Australia (Darwin) and South America (Rio de Janeiro). Botanic gardens on islands were created as early as the 18th century whereas those on the continental land masses, particularly mainland Africa, much later (Cronk & Fuller 1995). The importance of Bogor (formerly Bruitenzorg) in Indonesia has been emphasised by Bouvier (1946). The main purpose of these gardens was to introduce exotic seeds and plants (e.g. Darwin, Miller & Lonsdale 1987) and usually to assess the commercial potential of a variety of crops. The name given by the Germans to what is now known as the Limbe Botanic Gardens, was the 'Research Institute for Land Improvement' (Timler & Zepernick 1987), and clearly indicates the original purpose of the gardens. A lack of knowledge of the local timber trees was often the reason for introducing exotic tree species. During the early years of these tropical gardens the botanical interest was secondary.

However, many differences in the patterns of introductions, resulting chiefly from different colonial histories and geographical locations, are likely. It is known that Polynesians introduced a large number of woody plants to the Hawaiian islands prior to European colonisation (Wagner *et al.* 1990, Bevacqua 1994). Botanical gardens were established in settled areas - the easily accessible or climatically ideal regions near coasts or in cooler upland areas. Large areas of South America were devoid of settlements and thus botanic gardens and forestry trial plots until comparatively recently. The colonial powers had different routes for the introduction of plant material. Often plants were first transported to Europe (e.g. to Kew, Bruxelles, Berlin-Dahlem for respectively Britain, Belgium and Germany) and then disseminated to tropical gardens in their respective colonial territories.

During the past hundred years Africa has probably been subjected to less introduction of ornamentals than economically more advanced areas such as Australia and Hawaii which have developed major horticultural industries.

3.2 HUMAN PERCEPTION, IGNORANCE AND EXPERIENCE

Nearly all introductions of woody plants, which have become invasive, have been introduced intentionally by horticulturalists, botanists, foresters or gardeners. The bibliographical data showed that as early as last century a number of authors realised the regeneration potential and sometimes the invasive potential of introduced woody plants. These problems having been known for quite some time, it is then important to investigate how aware practitioners of introductions were of the potential problems associated with species introductions.

Botanists, conservationists, foresters, agroforesters and horticulturalists have, and often still are, to varying degrees, responsible for the introduction and planting of woody species. While there was awareness of invasive potential and related environmental impact, it appears that often it has been considered that introduction of potentially invasive species would do more good than harm. A number of examples are given below to illustrate the problem. In our view, many more cases could also be documented.

The French botanist Auguste Chevalier (1952) recommended the introduction of *Chromolaena odorata* to West Africa to control *Imperata* spp. and other coarse grasses despite the fact that he regarded the species as a weed (Chevalier 1949) and much earlier had published a paper on man's role in the dispersal of tropical plants (Chevalier 1931). A number of species introduced to tropical botanical gardens have become invasive but there is no evidence to show that scientists responsible for their introductions were aware of the potential problems. The appearance of articles warning that tropical botanical gardens could be the source of invasive species is a very recent development (Sheil 1994). However, Miller & Lonsdale (1987) have shown that the weedy nature and associated problem of introduced species at the Darwin Botanic Gardens was recognised early this century, but the botanists still failed to foresee the implications for the vegetation of the Darwin region.

During the 1980s it was realised that a number of introduced trees were spreading in the logged and natural forests of the East Usambaras in Tanzania (Binggeli & Hamilton 1990). Because the biological importance of the East Usambaras and the threat posed by logging, deforestation and invasive species an IUCN project was initiated to help in the sustainable management the mountains. One aspect of the programme consisted in rehabilitating or demarcating Forest Reserves to prevent forest encroachment. In order to make the demarcation noticeable exotics including species known to be invading the natural forest, such as *Cedrela odorata,* were planted.

The original vegetation, rich in endemic species, of the isolated Atlantic island of St Helena has almost entirely been destroyed. These changes have been induced by browsing, grazing, wood harvesting, forest clearance and plant introductions (Cronk 1989). On many parts of this rugged island this has resulted in severe soil erosion. In the early 1990s a sustainable development strategy was initiated by Overseas Development Agency to address St Helena's environmental problems. In their final report Spooner *et al*. (1993) give a list of exotic species colonising eroded areas which they classify as useful, neutral and some which may lead to resource degradation. The latter group include a species which may have adverse effect on soils and another is an unpopular weed. The colonisation potential of other introduced species is not discussed and assumed to be positive. It is even stated that *Acacia* used in afforestation "are growing well, but there is limited seedling colonisation outside the planted zones" indicating that the lack of natural regeneration is considered to be a negative feature and concluded that "a high research priority should be given to identifying the regeneration requirements and constraints of the different colonists." Although new species have been recommended for introduction, Spooner *et al*. (1993) give no clear justification for new imports and trials of *Leucaena* for fodder and *Casuarina equisetifolia* currently under way, two species well known for their invasive potential.

There is evidence from the temperate zone that some woody species (e.g. *Ulex europaeus*, *Lupinus arboreus*) facilitate the establishment of native forest. However this evidence is entirely lacking for the tropics and it is generally accepted that invasive plants displace rather than facilitate succession on tropical oceanic islands. Thus nitrogen-fixing plants such as *Acacia* and *Casuarina* spp. main be successfully used to prevent soil erosion but there is, at present, no evidence that they will eventually encourage the regeneration of native plants and that of endemic plants in particular.

Until recently foresters have expressed little concern about the invasive potential of introduced trees. In 1980, a book (Anon. 1980, 1983) on the choices of species to be used for fuelwood production globally and their silviculture was produced by BOSTID (Board on Sciences and Technology for International Development). For most species the ease of natural regeneration is discussed without indicating the geographical areas where prolific regeneration could lead to a weed problem. In fact about half of the species included are known to be invasive and some being serious pests in parts of the world. The authors were aware of the invasive problem but simply dealt with it by inserting a "warning" on the page facing the table of contents consisting of a single paragraph. In recent years all foresters have been aware of the invasive potential of some of their introductions and some have now started to confront the problem (e.g. Hughes & Styles 1986, Hughes 1994).

In India, due to its prolific natural regeneration *Leucaena leucocephala,* is generally considered to be a weed, yet it was planted, mainly as a fodder crop, in the Karnataka region in early 1980. Within ten years Patil & Kumar (1990) reported that the species had become a problematic weed in cultivated land, even today, new introductions of *Leucaena* germplasm are proceeding.

With respect to invasive species, little information from horticulture is readily available in the literature. Yet most invasive species have been introduced for ornamental purposes and this area necessitates much more attention. In many countries the introduction of species for ornamental purposes is subject to little regulations and is under-reported. A perusal of the B&T World Seeds Master List (Anon. 1996) indicate that seeds of around 50% of the species included in the Species Database can be readily ordered. As B&T World Seeds can supply reproductive material for around 35,000 species or cultivars the potential for the introduction of known and potential invasives is enormous.

A major source of ambiguity in many references to invasive species is taxonomic instability. This is compounded by poor historical records, uncertainty of the sources of introductions and frequent use of local rather than scientific names.

Species have sometimes been wrongly identified. For instance, In Hawai'i *Melaleuca quinquenervia* was formerly referred to as *M. leucadendron* which is not synonymous (Little & Skolmen 1989). Species identification can be difficult as a number of species hybridize readily. These taxonomic difficulties have been dealt with in some detail by a number of authors including Stirton (1979) and Swarbrick (1986).

In many cases taxonomically difficult groups are involved. Species of the genus *Cecropia* have been introduced to many parts of the tropics and are spreading spontaneously. Cases reported include *C. peltata* in Malaysia, Cameroon and Ivory Coast (Putz & Holbrook 1988, McKey 1988, Ake Assi 1979), *C. leucocoma* in Zaire (Léonard 1951) and *C. schreberiana* in Madagascar (C.C. Berg pers. comm. 1995). However, there is confusion about the identity of the various invading populations. Species in the genus *Cecropia* have strong morphological similarities but have somewhat distinct geographical and/or ecological ranges. The species *C. peltata* s.s. (central America), *C. pachystachya* (southern America) and *C. concolor* (Amazon basin) can be regarded as *C. peltata* s.l. The names given in the literature are sometimes inaccurate. Only when the origin of the material is known, is it possible to identify the specimen with confidence. Thus, in Madagascar *C. schreberiana* (native to the Caribbean) has often misidentified as *C. peltata*, although clear morphological differences exist between these two species. The *Cecropia* species reported from Zaire as *C. leucocoma* and from Malaysia as *C. peltata* have both recently proved to be *C. pachystachya*. The identity of the further African material remains unclear (C.C. Berg pers. comm. 1995). In Hawaii *C. obtusifolia* has also been erroneously identified as *C. peltata* (Wagner *et al*. 1990).

Details of early introductions are often vague in the extreme. Some species are initially described as native and only much later is their true origin discovered. For instance *Ocotea angustitepala* (Lauraceae), collected in 1912 in undisturbed forest (Robyns & Wylczek 1950), was described from Cameroon as a new species. It was later discovered to be a neotropical plant (*Ocotea patens*) introduced to the Victoria (Limbe) Botanic Gardens (Rowher 1989). Evidently, the species started to spread into natural forests soon after its introduction. Its current status in native vegetation is unknown. For a number of species which have been clearly shown to be spreading it is difficult, if not impossible, to determine whether they result from natural or human dispersal. These species reached new areas prior to the 19th century. Uncertainty concerning their status arises from the dearth of historical records. For instance, in the tropics it has been suggested that *Hibiscus schizopetalus* (Malvaceae) in Tanzania (Hawthorne 1993) and *Ceiba pentandra* (Bombacaceae) in Africa (Irvine 1961) are invaders, whereas *Mora excelsa* (Caesalpiniaceae) in Trinidad migrated naturally (Beard 1945).

The status of *Mimosa pigra* in the tropics is a good illustration of the difficulties in establishing the introduction and spread of a woody invasive plant. *M. pigra* originated from tropical America and was apparently widespread in tropical Africa by the mid 19th century. It has been suggested that its seeds floated across the Atlantic ocean, however as the seed-pod sections float by surface tension rather than buoyancy they are unlikely to travel such a long distance. Therefore the introduction to and the widespread distribution of *M. pigra* in Africa remains a mystery (Lonsdale *et al*. 1989). It was originally thought that *M. pigra* had been introduced to Northern Australia in the late 1930s but subsequent detailed investigations of photographs and grey literature by Miller & Lonsdale (1987) suggest that the shrub was introduced prior to 1891. Early accounts referred to *M. rubicaulis*, a misnomer for *M. pigra* or simply as mimosa and already referred to the species weediness. The case of *M. pigra* clearly shows that painstaking investigations are necessary to unravel some of the historical aspects of an invader.

Woody plant species introduced for crop purposes usually have a set of characteristics which include very fast growth, ease of propagation (including suitability for aerial seeding), were often nitrogen fixers and resistant to a variety of biotic and abiotic agents such as pests and diseases, aperiodic drought, inundation and fire (e.g. Maydell von 1989, Hughes 1994). The view is bluntly expressed by Vietmeyer (1986) writing about the *Casuarina* invasion of Florida where, in his view, the tree's "aggressiveness is a threat, not a benefit" he adds: "But isn't an unstoppable tree just what we need? in our deforested world the whole idea of a 'weed tree' seems like a paradox. If anything, weed trees are vital to the planet's future. Adaptable, resilient, irrepressible, resistant to disease - what could be more vital for Ethiopia, Chad, Nepal, Haiti, and the other bedrock spots of environmental degradation where the people are too busy trying to survive to worry about nurturing trees?" In parts of semi-arid western Africa the local population's main reasons for preferring *Azadirachta indica* for single tree planting is a combination of good availability of seedlings and the ease of vegetative propagation, fast growth and low risk as well as shade and insect repellence (von Maydell 1989) .

3.3 INVASIVE TENDENCIES AND SPECIES BIOLOGY

In the Invasive Woody Plant Database the purpose and date of the original introduction are included. However, the database does not contain any information on secondary introductions or plantings or on the use of a species for other purposes than the original introduction. The original introduction is usually limited to a very small number of plants often in a botanic garden or an experimental plot or a private garden. A close look at many cases of invasive species show that secondary introductions or plantings were usually carried out on a very large scale much later than the original introduction. In Hawaii seeds of many tree species introduced for ornamental purposes prior to or around 1900 were aerially sown in the 1920s and 1930s for forestry purposes (Little & Skolmen 1989). Similarly in Tanzania *Maesopsis eminii* was widely planted 50 years after its original introductions (Binggeli 1989). This has several implications including: artificial dispersal to new sites and rapid build up of a very large population of seed producing trees. This might explain the time-lag (see below) observed between the introduction and the start of the invasion of some woody species.

It has been estimated that only about 1% of introduced species become invasive (e.g. Groves 1986). The reasons why most introduced species do not become invasive are not known. Suggestions for a certain number of species can be made which apply to the tropics but may be less relevant to the temperate zone. In tropical regions most widely introduced species have some sort of commercial value whereas potentially valuable species, ornamentals or botanically interesting plants have been introduced rather locally in a few botanic gardens. *Cecropia peltata* is an escape from the Limbe Botanic Gardens (Cameroon) and is now competing with *Musanga cecropioides* in secondary vegetation (McKey 1988). This species was also introduced to the Amani Botanic Gardens (Tanzania). However, Fernie (1948) reported that only one tree survived at Amani, and as the species is dioecious, it cannot spread even with suitable environmental conditions.

A number of fast growing introduced tropical trees have exhibited invasive tendencies. Janzen (1986) has argued that many of these species, including a large number of legumes, are the sort of species which can become invasive and have a strong impact on the rate of succession and the species composition of the vegetation. However, species of extensively planted genera such as *Eucalyptus* and *Tectona* have caused few problems. In the Sierra of southern Peru *Eucalyptus globulus* is the dominant tree at most altitudes and essential to the local economy (Dickinson 1969). Yet, it does not regenerate. Although a few hundred species of *Eucalyptus* have been introduced and often extensively planted throughout the world (Penfold & Willis 1961), few instances of invasions have been reported and, those which have, tend to be relatively minor (Kirkpatrick 1977). Abandoned logged *Eucalyptus tereticornis* in the Western Ghats (India) show that although the species fails to regenerate, its coppicing ability allows it to remain dominant in the secondary regrowth (George *et al*. 1993) but the understorey species composition suggest that the typical complement of native species will eventually dominate the canopy. Kirkpatrick (1977) identified the poor dispersal ability of *Eucalyptus* combined with scattered distribution of suitable habitats for seedling survival as the reason for the very slow spread of *Eucalyptus* species in California. Seedling establishment is only successful in areas more or less free from plant competition. The observed limited spread has occurred despite various species being widely used for timber, windbreak and ornamental purposes.

Until recently the problem of invasive woody plants has been publicized principally in relation to oceanic islands such as Hawai'i (e.g. Stone *et al*. 1992), Rodrigues (Strahm 1989), Réunion (Macdonald *et al*. 1991) and Madagascar (Sussman & Rakotozafy 1994). In recent years a number of invasive species have been reported from Africa (Binggeli & Hamilton 1993, Sheil 1994), Australia (Swarbrick & Skarrett, 1994) and India (Saxena 1991). It has now been realised that biological invasions may become a serious and ever-increasing problem in some continental regions. Below a number of reasons are given for tendencies for such species to become increasingly problematical. These reasons are mainly related to increasing direct and indirect human induced disturbance and to human ever-increasing use of nature. Some evidence supporting some of these views have recently been reported.

- Large gaps created by logging operations appear to be more readily invaded by exotics than natural tree fall gaps. The shrub *Chromolaena odorata* is readily found in selectively logged forests of the Western Ghats (India) but absent from natural forest (Chandrashekara & Ramakrishnan 1994). The reason for this is probably due to the fact *C. odorata* seeds are usually locally wind-dispersed but can be readily transported by vehicles (see species account). In heavily exploited and degraded forests of lowland of southwestern Sri Lanka *Alstonia macrophylla* (Apocynaceae) is commonly found in large gaps but appear to be absent from unlogged forest. In Tanzania *Maesopsis eminii* becomes dominant in logged forest but is capable of regenerating in natural forests in large treefall gaps. In the same forests the shrub *Clidemia hirta* is also becoming quite common in natural forest gaps.

- Why do exotics matter in the general context of conservation of biodiversity? Increase in turn-over rate has been observed (Phillips & Gentry 1994; Phillips *et al*., 1994), potential rapid climatic change should result in increased intensity of disturbance, increased human pressure for firewood and forest products will all lead to conditions more favourable to known invasive woody species. Most of these species require a substantial amount of disturbance to spread extensively.
- If climate changes many areas of natural vegetation are isolated and species will fail to move to other islands.
- The conservation of biodiversity becomes increasingly significant in disturbed areas as areas of natural or semi-natural vegetation steadily decrease. In an overpopulated and resource hungry world secondary vegetation will become more and more important to the conservation of biodiversity. For instance in the British Isles motorway verges, railway embankments and abandoned quarries are now important assets to nature conservation.
- Susceptibility of natural areas to invasions is higher if a large seed source is available around it. The smaller the area of natural vegetation the more likely it is to be invaded.
- Data available from the tropics and sub-tropics on the incidence of invasions clearly show a higher reported number of cases in areas with more advanced economies and standards of living. This is probably not coincidental and rather reflects the large number of plants introduced and distributed in large numbers over wide geographical range for ornamental purposes. Assuming that the less developed world will increase its standards of living an ever increasing number of exotics species will be introduced to regions hitherto not widely affected by invasive species.

A combination of isolated natural areas surrounded by large tracts of potentially invasive species, higher human disturbance, higher natural disturbance, increased movement of exotic plants and potential impact of rapid climatic change (more important in areas without climatic gradients) will undoubtedly lead to an increased threat by introduced species.

3.4 TIME-LAGS

The populations of introduced species often remain small and localized for long periods of time before they exhibit very rapid expansion. Until very recently little evidence was available to support a number hypothetical explanations for these observed time-lags or lag phases. The reasons for these time-lags are threefold (Hobbs & Humphries 1995):

- genotypic adaptations
- cyclical disturbance or a combination of environmental conditions
- species, with exponential growth, not observed until the population reaches a critical size.

The time between the introduction of a species and its first record of spread and pest status in tropical invasive woody species varies, respectively, from 3 years to around 50 years and from 4 years to around 90 years (Table 3.4.1). Most woody plant species were introduced between 1838 and 1937 with a peak in the late 19th century. No obvious differences are observed when the degree of invasiveness is taken into account. This data further supports the view that the existence as well as the duration of time-lags is highly variable. A species may quickly become highly invasive (DI = 3) even after it has already been present for a long-time in a particular region.

In the tropics time-lags appear to be much shorter (Table 3.4.1) than those observed in temperate species. Kowarik (1995) reported that in the German Brandenburg province the average duration of the time-lag between the introduction and the initiation of an invasion was 131 years and 170 years for, respectively, shrubs and trees.

Table 3.4.1. Duration (in years) of known time-lags between the introduction and first spread and pest status in tropical invasive woody plants.

	Region	Year of initial introduction	noticed after (yrs)	Perceived as problem/pest after (yrs)
Acacia nilotica	N. Australia	ca 1900	ca 50	ca 57
Casuarina equisetifolia	Florida	ca 1900	ca 56	ca 65
Cecropia peltata	Ivory Coast	1910	<48	69
	Cameroon	ca 1910	ca 23	ca 36
	Zaire	1911	19	40
	Malaysia	1953	19	35
Chromolaena odorata	Ivory Coast	ca 1955	ca 7	ca 20
Cinchona succirubra	Galapagos	1946	26	40
Lantana camara	Galapagos	1938	32	40
Maesopsis eminii	East Africa	1913	14	65
Miconia calvescens	Hawaii	ca 1975	ca 16	ca 16
Mimosa pigra	N. Australia	ca 1880	ca 36	ca 90
Pittosporum undulatum	Jamaica	1883	ca 60	105
Psidium guajava	Galapagos	1858	?	< 90
Rubus sp.	Galapagos	1983	3	4
Schinus terebinthifolius	Florida	1898	50	75

FACTORS DETERMINING TIME-LAGS

For a number of the more comprehensively documented species reasons for the observed time-lags have been inferred and sometimes demonstrated (Table 3.4.2). All reported instances show that major changes in biotic and abiotic factors determine the duration of time-lags.

Abiotic factors include wind, flooding and deforestation. In the case of *Acacia nilotica* in Australia the time-lag resulted from a series of above average wet years in the early 1950s. In Florida *Casuarina equisetifolia* started spreading following the disturbance caused by two hurricanes. *Cecropia peltata* was introduced to south western Ivory Coast as a shade tree in coffee plantations in 1910. By the late 1950s the species had spread by 20 km. However, following the destruction of most of the remaining forest the rate of spread increased markedly in the 1960s: the species had reached sites 100 km away from where it was introduced.

The introduction of pollinators, marked changes in grazing and trampling intensities are examples of biotic factors determining the duration of time-lags. The sudden introduction of a pollinating agent is one of the main biotic factor determining some time-lags. For instance, *Ficus microcarpa* widely planted as an ornamental in Florida only became a pest about 45 years after introduction, when its natural pollinator - the fig wasp (*Parapristina verticillata*) was introduced. Although no evidence for the existence of genetic adaptations in determining time-lags is available for the tropics, limited data from the temperate zone indicate that this factor is probably of some importance in tropical regions too. It has been shown for the Chinese ornamental tree, *Ailanthus altissima,* introduced to and widely planted in North America, that native and introduced populations are genetically different although their genetic variability is the same. However, it has been argued that the differences are the result of human selection rather than adaptation to local environmental conditions.

A number of other biotic and abiotic factors may also affect time-lags and are well-known to produce marked increases in woody plant population sizes including drought, frost, human-induced disturbance, hybridization and diseases.

It is often difficult and even impossible to judge if there is a time-lag or simply marked increases in population size resulting from various biotic and abiotic factors - examples are given in Table 3.4.2. In the case of *Pittosporum undulatum* spread into the natural forest only started after hurricane disturbance, although it had already invaded disturbed forest.

In many cases the original introduction of a woody species was limited to one or a few individuals, but a number of subsequent introductions, usually consisting of many individuals, were made for a different purpose. For instance, in Hawaii and Florida a few individuals of some tree species were planted as ornamentals but decades later the same species were either widely planted in forestry plantations or large quantities of seeds were aerially sown. Some of these species were observed to spread only following these secondary introductions.

In areas where monitoring is not regular some time-lags will be an artifact of erratic recording interest.

Table 3.4.2. Biotic and abiotic factors known to influence or determine the time-lag and marked population increase of invasive woody plants in the tropics.

	time-lag	marked population increase
ABIOTIC FACTORS		
Logging/deforestation	*Cecropia peltata*	*Maesopsis eminii*
Wind - hurricane	*Casuarina equisetifolia*	*Pittosporum undulatum*
- treefall		*Passiflora mollissima*
Flooding	*Acacia nilotica*	
	Mimosa pigra	
Fire		*Chromolaena odorata*
	Pinus pinaster	
Nutrient enrichment		*Schinus terebinthifolius*
BIOTIC FACTORS		
Pollinator	*Ficus microcarpa*	
Grazing	*Ulex europaeus*	
Disperser		*Psidium guajava*
Digging by mammals		*Clidemia hirta*
	Passiflora mollissima	
Trampling by mammals	*Ulex europaeus*	

Table 3.4.3. Age (years) of first reproduction of tropical invasive woody species.

Age	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	no data
Frequency	8	6	3	1	4	-	1	-	-	3	-	-	-	-	1	218

SUCCESSIONAL STATUS AND DISTURBANCE

Most short time-lags (i.e. <10-15 years) are caused by a lack of seed production resulting from the juvenile state of the plants. Although limited, the available data indicate that under favourable conditions most species start sexually reproducing by the time they are 10 years old (Table 3.4.3). Longer time-lags, observed in a number of species, are essentially consequences of major, and often dramatic, disturbance events (e.g. hurricane, flood, fire...) which create the conditions favouring prolific regeneration (invasion windows). When an introduced species requires a particular form and/or intensity of disturbance occurring at irregular intervals the time-lag is variable.

Early successional species, which exhibit early and yearly fruiting and efficient dispersal, and/or massive seed banks, are able to exploit invasion windows created by exceptional disturbance events. Species with irregular fruiting and no seed bank will often fail to regenerate every time suitable conditions arise and one or more invasion windows may be necessary before the species spread.

Considering that the majority of tropical woody species have been introduced within the last hundred years and included relatively few late-successional tree species (usually not used in amenity planting and forestry) it is not surprising that few of these species have been reported as invading tropical regions. In the temperate zone several late successional species are now spreading into semi-natural vegetation (e.g. *Quercus rubra*, *Prunus serotina* and several conifers).

The duration of the phase between the introduction of a species and its spread being so variable it is not possible to be certain that a species, although present for several decades, will not spread. For any particular region it is essential to understand the long-term disturbance regime as well as the autecology (inclusive of reproductive biology and regeneration requirements) of introduced species before any predictions can be made. Otherwise close monitoring of natural and semi/natural vegetation, particularly after exceptional disturbance events, is necessary for the early detection of new invasions.

3.5 MANAGEMENT AND POLICY IMPLICATIONS

Although much information has been gathered on biological invasions (e.g. Drake *et al.* 1989), our ability to identify potential invaders has been doubted (e.g. Crawley 1987). Willis (1991) in his review of Drake *et al.* (1989) suggested that some general pointers to the probability of a successful invasion: e.g. high habitat disturbance and broad ecological amplitude, short generation time, high reproductive output, high diffusivity and high numbers of invading individuals. However, these pointers do not explain why a species is a successful invader, although they may suggest factors which regulate the speed and extent of an invasion. Indeed, experimental work by Bergelson (1994) shows that fecundity may not be a useful predictor of invasiveness. A number of diverging views concerning the invasive potential of various plant species exist. For instance, Swarbrick (pers. comm. 1994) suggested that any species given the right location, climate and environment is potentially invasive, whereas it is often considered that pioneer and not 'climax' spp can become invasive (e.g. Whitmore 1991).

In Southern Africa, several biological invasions have proved problematical, Richardson & Cowling (1992) have offered a tentative flow diagram to distinguish between species with low and high probabilities of becoming invaders in the fynbos biome. Other work recently carried out on the subject of predictability has been carried out on plants introduced to North American and Australia and on the genus *Pinus*. Reichard (1994) compared 235 invasive plant species with 114 introduced species which have failed to spread and found that the best single predictor for invasiveness was the behaviour of the species in other regions where it has been introduced: once an invasive, often an invasive.

Using multiple logistic regressions Scott & Panetta (1993) found that for agricultural weeds introduced from southern Africa to Australia the highest level of variation was explained by weed status in native region. Using their regressions Scott & Panetta (1993) predict the future weed status of a number of recently arrived or not yet introduced species. However no suitable predictor of invasive plants (environmental weeds) were identified.

Rejmánek & Richardson (1996) by using a discriminant function, conclude that invasiveness in the genus *Pinus* can be predicted from three characteristics: mean seed mass, minimum length of the juvenile period and mean interval between large seed crops. They found that short juvenile phase, small seed mass and short intervals between large seed crops are predictive traits of invasive pine species. They then suggest that their discriminant function derived from demographic parameters of pines can be used as a general screening tool for the detection of invasive woody seed plants. Using their discriminant function they correctly classified 38 out of 40 invasive species as invasive. As the two exceptions were due to efficient vertebrate dispersal and concluded that this factor should be taken into account. They then tested cultivated but non-invasive plants which were all correctly classified as non-invasive. However out of 13 species or genera thought to be non-invasive by Rejmánek & Richardson 6 are recorded as potentially or moderately invasive in the Invasive Woody Plant Database! Clearly further work needs to be carried out to extend Rejmánek & Richardson's pine predictions to other woody plants. One major difficulty is that one of their predictors, interval between seed crops, is generally poorly known or unknown. This characteristic has not been included in the Invasive Woody Plant Database due to the scarcity of reliable information. Although included in the database, information on the age of first reproduction (phase change) is available for fewer than 50 of the invasive woody plants. At present the database cannot be used to test the applicability of Rejmánek & Richardson's predictions to other woody plants.

Vegetative propagation is the main, if not the only, mean of spread of a number of invasive woody plants and this is ignored by Rejmánek & Richardson. It is likely that Rejmánek & Richardson criteria will eventually proved not to be applicable to most woody plants and that families and even genera will need to be investigated independently. At present, species known to be invasive elsewhere in the world under similar climatic conditions is still the best predictor of invasiveness.

Considering the difficulty in predicting the invasive potential of introduced species, it is therefore essential to look at the reasons and justifications for introducing plant species. Hughes (1994) has extensively discussed the pros and cons of species introductions and provided guidelines for the introduction or non-introduction of non native species. Carter (1994) has suggested that "all plant introductions should be presumed weeds until proven otherwise" and that a plant introduction protocol should be set up, based on the methodology used in the introduction of biological control agents. In case the introduction of a new species is the only mean to satisfactorily fulfil a long-term need, Hughes (1994) suggested that it is then essential to make that its invasive potential will be as limited as possible. Procedures to reduce the risk of introducing a potentially invasive species should include extensive information searches prior to the proposed introduction and the establishment of limited trial plantings.

All introductions of non-indigenous plant species should be screened with great care in a process which considered the status in the native range and at other points of introduction. The following points require particular attention and should rapidly provide a clear indication to the introduced species invasive potential.

a. Has the species or a related species has been reported as invasive elsewhere?

b. How similar is the site of the proposed introduction to that of the species in its native and invaded regions? This includes comparisons of soil, climate, disturbance (both in terms of intensity and periodicity including that of fire, wind, flood) and human disturbance. Conditions favouring or limiting the species spread should be identified.

c. Knowledge of the species reproductive biology is important and in particular that of seed production, seed longevity, and dispersal ability.

d. Susceptibility of young individuals to grazing (e.g. whether the plant is thorny or not),

e. Assessment of practical and effective methods of control in the case of weediness problems. The economics of control must be carefully considered.

If the above points indicate that the proposed species has no invasive potential an introduction may be considered. On the other hand if the proposed species exhibits invasive tendencies a strong justifications will have to be made for its introduction.

If a species introduction is initiated following the assessment of its invasive potential, then tests trials should be carried out. These trials should be established at some distance from natural vegetation and have a clear buffer zone. This buffer zone . The field trials would assess the following parts of the plant's reproductive cycle over a few years after the species has started producing viable seeds:

- seed production.
- germination requirements under varied environmental and climatic conditions.
- seedling establishment in a number of habitats and disturbance regime.

It is also important to establish why an introduced species fails to produce any seeds. This might be due to the absence of pollinator (see the case of *Ficus* above) or a period of unusual unfavourable climatic conditions.

Carter (1994) identified a number of difficulties with screening of plants in this way. These include:

- unpredictable behaviour of the introduced species after removal from native pathogens, insects and browse animals,
- unpredictable behaviour under new climatic, management and fire regimes, and
- genetic drift or hybridization which may change the character of the plant introduced. Thus it is essential that, once species are introduced, there should be:
- Long-term and regular monitoring (problems may not show for 100 years, see time-lags above), and
- rapid action if weediness appears a problem.

Case studies reported by Waterhouse (1994) on *Chromolaena odorata* in Northern Australia, Loope *et al*. (1992) on *Miconia calvescens* in Hawaii and Wester & Wood (1977) on *Clidemia hirta* in Fiji and Hawaii clearly show that in the case of highly invasive species, eradication is possible if the invader is controlled at a very early stage of the invasion. Once a plant has become a weed it is usually impossible to eradicate it (Carter 1994).

The following points are essential in detecting the early stages in an invasion:

1. awareness that the species is a problem in another region where climatic and environmental factors are similar,
2. first-hand knowledge in identifying and recognizing the species in the wild is essential, and
3. active governmental or voluntary organisation in the field of plant invasions is necessary to provide background response.

The above three points require resources, a good and extensive higher level educational system, good environmental awareness (particularly of biological invasions) as well as an efficient information system. At present the information system is a problem worldwide and the setting up of database(s) on invasive species is being considered or set up by various national and international bodies . Awareness exist in regions where many highly invasive species have already altered the ecosystem structure and function. Resources and to an extensive education system are only available in richer countries.

The problem of invasive plants is more likely to become more severe rather than recede in the coming decades. At the same time resources available to deal with the problem of invasive plants are unlikely to increase significantly. Only by using resources, not just financial but also intellectual, more efficiently will be there be more progress made to control invaders. Muniappan & Viraktamath (1993) have pointed out that the effort to control invasive plants in India has been sporadic and uncoordinated. They stress that to deal with the problem of invasive plants cooperative projects must be undertaken by researchers with a variety of scientific backgrounds. In fact Muniappan & Viraktamath's remarks do not just apply to India but is highly relevant to scientists worldwide. As plant introductions and invasions are a global problem coordination and communication must be tackle with on a global scale.

3.6 RESEARCH NEEDS

One of the main problems relating to invasive woody plants and plant introductions is a lack of fundamental knowledge of the basic characteristics of woody plant species as well as the lack of an efficient and easily accessible international information system. Furthermore the type and amount of information required by various professionals varies immensely.

INFORMATION SYSTEM

There is a need for an efficient information system which should provide the following information:

a. current distribution, habitat type and degree of invasiveness of woody plant species.
b. bibliographical resources including the supply of relevant literature.
c. control methods including by mechanical, chemical and biological means.
d. directory of people and organisations involved in the study and control of particular woody species.
e. provide species accounts on all highly and a number of moderately invasive woody species

FUNDAMENTAL RESEARCH

The assessment of the invasive potential of a species and the control of invaders can only be successful if detailed knowledge of the autecology of the invader and the invaded ecosystem is available. This information is either not available or difficult to obtain. The following areas of research require special attention:

a. species autecology with special reference to the reproductive cycle including dispersal ability. Studies must be carried out in both the native and invaded regions.

b. ecosystem dynamics but particularly the variation in space, time and intensity of disturbance and its impact on species composition and population densities.

c. impact of potential climate change on invading species and on introduced, but non invasive, species. Further work on prediction of invasibility is required.

d. The characteristics of invasive species need to be investigated in more detail and should be compared to control groups such as a sub-set of local floras and to introduced but non-invasive plants. Stratification of the data based on lifeform and uses may proved advantageous.

e. more efficient control procedures and field methods need to be designed.

4 PROVISIONAL LIST OF INVASIVE WOODY PLANTS IN TROPICAL AND SUB-TROPICAL REGIONS

Provisional list (1 / 6 / 1997) of woody plant species invasive in the tropics and the sub-tropics. Species are listed according to life form and degree of invasiveness (DI). Species with an ***** are dealt with in detail in the species accounts. Nomenclature follows mainly Mabberley (1987). The information included below is based on the original papers and the taxonomic status has been updated whenever possible but undoubtedly errors remain (P. Binggeli, p.binggeli@ulst.ac.uk, would appreciate any critical comments and suggestions in order to upgrade the list).

The most exhaustive list of weedy plants, containing over 16,000 records, has been produced by Rod Randall. This weed list is complimentary to the one given here. It includes woody and non-woody plants worlwide but its coverage of Australia is more comprehensive than that of the rest of the world.

http://www.agric.wa.gov.au/progserv/plants/weeds/weeds/weedlist.htm

(Degree of invasiveness (DI): 1 = possibly/potentially invasive, 2 = moderately invasive, 3 = highly invasive, see section 2.3.2.2 for details).

TREES >15m tall

GENUS	SPECIES	AUTHORITY	FAMILY	DI
Acacia	auriculiformis	A. Cunn. ex Benth.	Mimosaceae	3
Acacia	dealbata	Link	Mimosaceae	3
Acacia	mearnsii	De Wild.	Mimosaceae	3
***** Acacia	nilotica	(L.) Del.	Mimosaceae	3
***** Casuarina	equisetifolia	L.	Casuarinaceae	3
Casuarina	glauca	Siebold ex Sprengel	Casuarinaceae	3
***** Cecropia	peltata	L.	Cecropiaceae	3
Litsea	glutinosa	(Lour.) C.B. Robinson	Lauraceae	3
***** Maesopsis	eminii	Engler	Rhamnaceae	3
***** Melaleuca	quinquenervia	(Cav.) S.T. Blake	Myrtaceae	3
***** Pinus	patula	Schlecht. & Cham.	Pinaceae	2
Pithecellobium	dulce	(Roxb.) Benth.	Mimosaceae	3
***** Pittosporum	undulatum	Vent.	Pittosporaceae	3
Ravenala	madagascariensis	Sonnerat	Musaceae	3
Acacia	confusa	Merr.	Mimosaceae	2
Albizia	falcataria	(L.) Fosb.	Mimosaceae	2
Albizia	lebbeck	(L.) Benth.	Mimosaceae	2
Aleurites	moluccana	(L.) Willd.	Euphorbiaceae	2
Araucaria	angustifolia	(Bertol.) Kuntze	Araucariaceae	2
Azadirachta	indica	A. Juss.	Meliaceae	2
Bauhinia	monandra	Kurz.	Caesalpiniaceae	2
Bischofia	javanica	Blume	Euphorbiaceae	2
Blighia	sapida	König	Sapindaceae	2
Broussonetia	papyrifera	(L.) Vent.	Moraceae	2
Cassia	siamea	Lam.	Caesalpiniaceae	2

Cedrela	odorata	L.	Meliaceae	2
Cinnamomum	camphora	(L.) Nees & Eberm	Lauraceae	2
Cinnamomum	zeylanicum	Breyn	Lauraceae	2
Colophospermum	mopane	(Benth.) Léonard	Caesalpiniaceae	2
Eucalyptus	camaldulensis	Dehnh.	Myrtaceae	2
Eucalyptus	deglupta	Blume	Myrtaceae	2
Eucalyptus	robusta	Sm.	Myrtaceae	2
Ficus	microcarpa	L.f.	Moraceae	2
Ficus	religiosa	L.	Moraceae	2
Flindersia	brayleyana	F. Muell.	Rutaceae	2
Fraxinus	uhdei	(Wenzig) Lingelsheim	Oleaceae	2
Gmelina	arborea	Roxb.	Verbenaceae	2
Grevillea	robusta	Cunn.	Proteaceae	2
Harungana	madagascariensis	Lam. ex Poiret	Guttiferae	2
Heliocarpus	popayanensis	HBK.	Tiliaceae	2
Ilex	aquifolium	L.	Aquifoliaceae	2
Litsea	monopetala	(Roxb.) Pers.	Lauraceae	2
Mangifera	indica	L.	Anacardiaceae	2
Manilkara	zapota	(L.) P. Royen	Sapotaceae	2
Melia	azedarach	L.	Meliaceae	2
Melicoccus	bijugatus	Jacq.	Sapindaceae	2
Milletia	dura	Dunn	Papilionaceae	2
Ochroma	pyramidale	(Cav. ex Lam.) Urban	Bombacaceae	2
Pandanus	tectorius	Park	Pandanaceae	2
Paraserianthes	falcataria	(L.) I. Nielsen	Mimosaceae	2
Phoenix	dactylifera	L.	Arecaceae	2
Pinus	lutchuensis	Mayer	Pinaceae	3
Pittosporum	viridiflorum	Sims	Pittosporaceae	2
Pongamia	pinnata	(L.) Pierre	Papilionaceae	2
Prosopis	pallida	(Humb.&Bonpl. ex Willd.) HBK.	Mimosaceae	2
Rhizophora	mangle	L.	Rhizopharaceae	2
Samanea	saman	(Jacq.) Merr.	Mimosaceae	2
Spathodea	campanulata	Beauv.	Bignoniaceae	2
Swietenia	mahagoni	(L.) Jacq.	Meliaceae	2
Syzygium	jambos	(L.) Alston	Myrtaceae	2
Tabebuia	pallida	(Lindley) Miers	Bignoniaceae	2
Tamarindus	indica	L.	Caesalpiniaceae	2
Terminalia	catappa	L.	Combretaceae	2
Terminalia	myriocarpa	Van Heurck & Müll. Arg.	Combretaceae	2
Toona	ciliata	M. Roemer	Meliaceae	2
Trema	orientalis	Blume	Ulmaceae	2
Achras	zapota	L.	Sapotaceae	1
Albizia	chinensis	(Obseck) Merr.	Mimosaceae	1
Ceiba	pentandra	(L.) Gaertn.	Bombacaceae	1

Cocos	nucifera	L.	Palmae	1
Enterolobium	saman		Mimosaceae	1
Eucalyptus	torelliana	F. Muell.	Myrtaceae	1
Inocarpus	fagiferus	(Park.) Fosberg	Papilionaceae	1
Swietenia	macrophylla	King	Meliaceae	1

SMALL TREES
15m< >5m

GENUS	SPECIES	AUTHORITY	FAMILY	DI
Acacia	decurrens	(J.C. Wendl.) Willd.	Mimosaceae	3
Acacia	saligna	(Labill.) H.L. Wend.	Mimosaceae	3
Cinchona	succirubra	Pavon ex Klotzsch	Rubiaceae	3
* Leucaena	leucocephala	(Lam.) De Wit	Mimosaceae	3
Ligustrum	robustum	Blume	Oleaceae	3
* Miconia	calvescens	DC.	Melastomataceae	3
* Mimosa	pigra	L.	Mimosaceae	3
* Myrica	faya	Ait.	Myricaceae	3
Parkinsonia	aculeata	L.	Caesalpiniaceae	3
Psidium	cattleianum	Sabine	Myrtaceae	3
* Psidium	guajava	L.	Myrtaceae	3
Schefflera	actinophylla	(Endl.) Harms	Araliaceae	3
* Schinus	terebinthifolius	Raddi	Anacardiaceae	3
Sesbania	punicea	(Cav.) Benth.	Mimosaceae	3
Solanum	mauritianum	Scopoli	Solanaceae	3
Syzygium	malaccense	(L.) Merr. & Perry	Myrtaceae	3
Tibouchina	urvilleana	(DC) Cogn.	Melastomataceae	3
Acacia	catechu	(L.f.) Willd.	Mimosaceae	2
Adenanthera	pavonina	L.	Mimosaceae	2
Aleurites	fordii	Hemsley	Euphorbiaceae	2
Anacardium	occidentale	L.	Anacardiaceae	2
Annona	squamosa	L.	Annonaceae	2
Ardisia	humilis	Vahl	Myrsinaceae	2
Caesalpinia	pulcherrima	(L.) Sw.	Caesalpiniaceae	2
Carica	papaya	L.	Caricaceae	2
Chrysobalanus	icaco	L.	Chrysobalanaceae	2
Cinchona	officinalis	L.	Rubiaceae	2
Cinchona	pubescens	Vahl	Rubiaceae	2
Citharexylum	caudatum	L.	Verbenaceae	2
Citrus	aurantiifolia	(Christm.) Swingle	Rutaceae	2
Citrus	aurantium	L.	Rutaceae	2
Citrus	limon	(L.) Burm. f.	Rutaceae	2

Citrus	reticulata	Blanco	Rutaceae	2
Citrus	sinensis	(L.) Osbeck	Rutaceae	2
Coccoloba	uvifera	(L.) L.	Polygonaceae	2
Coffea	arabica	L.	Rubiaceae	2
Cordyline	fruticosa	(L.) A. Chev.	Agavaceae	2
Corynocarpus	laevigata	Forster & Forster f.	Corynocarpaceae	2
Cyathea	cooperi	(Hook. ex F.Muell.) Dom.	Cyatheaceae	2
Cyphomandra	crassicaulis	(Cav.) Sendtn.	Solanaceae	2
Dalbergia	latifolia	Roxb.	Papilionaceae	2
Dalbergia	sissoo	Roxb. ex DC.	Papilionaceae	2
Delonix	regia	(Hook.) Raf.	Caesalpiniaceae	2
Eriobotrya	japonica	(Thunb.) Lindley	Rosaceae	2
Flacourtia	indica	(Burm. f.) Merr.	Flacourtiaceae	2
Grevillea	banksii	R. Br	Proteaceae	2
Hibiscus	schizopetalous	(Masters) Hook. f.	Malvaceae	2
Hibiscus	tiliaceus	L.	Malvaceae	2
Hovenia	dulcis	Thunb.	Rhamnaceae	2
Jacaranda	mimosifolia	D. Don	Bignoniaceae	2
Leptospermum	scoparium	Forster & Forster f.	Myrtaceae	2
Manihot	glaziovii	Muell. Arg.	Euphorbiaceae	2
Melaleuca	leucadendron	L.	Myrtaceae	2
Melochia	umbellata	(Houtt.) Staf.	Sterculiaceae	2
Mimosa	albida	Rudd.	Mimosaceae	2
Mimosa	nilotica	(L.) DeLisle	Mimosaceae	2
Mimosa	sepiaria		Mimosaceae	2
Morinda	citrifolia	L.	Rubiaceae	2
Moringa	oleifera	Lam.	Moringaceae	2
Muntingia	calabura	L.	Elaeocarpaceae	2
Olea	europaea	L.	Oleaceae	2
Ossaea	marginata	(Desr.) Triana	Melastomataceae	2
Persea	americana	Miller	Lauraceae	2
Phyllanthus	acidus	(L.) Skeels	Euphorbiaceae	2
Pinus	caribaea	Morelet	Pinaceae	2
Pithecellobium	unguis-cati	(L.) Benth.	Mimosaceae	2
Pittosporum	ferrugineum		Pittosporaceae	2
Poncirus	trifoliata	(L.) Raf.	Rutaceae	2
Prosopis	juliflora	(Sw.) DC.	Mimosaceae	2
Rhizophora	stylosa	Griff.	Rhizopharaceae	2
Sambucus	nigra	L.	Caprifoliaceae	2
Schinus	molle	L.	Anacardiaceae	2
Syzygium	cumini	(L.) Skeels	Myrtaceae	2
Terminalia	arjuna	(Roxb.) Beddome	Combretaceae	2
Trema	micrantha	Blume	Ulmaceae	2
Vitex	glabrata	R.Br.	Verbenaceae	2
Vitex	trifolia	L.	Verbenaceae	2

Bixa	orellana	L.	Bixaceae	1
Bruguiera	gymnorhiza	(L.) Lamk.	Rhizophoraceae	1
Cassia	spectabilis	DC.	Caesalpiniaceae	1
Cassia	suffructicosa	Koenig	Caesalpiniaceae	1
Cordia	sebestena	L.	Boraginaceae	1
Ilex	paraguariensis	A. St-Hil.	Aquifoliaceae	1
Rhododendron	arboreum	Sm.	Ericaceae	1
Sambucus	mexicana	K. Presl ex A. DC	Caprifoliaceae	1
Sesbania	sesban	(L.) Merrill	Mimosaceae	1
Tecoma	stans	(L.) Kunth	Bignonaceae	1
Ziziphus	mucronata	Willd.	Rhamnaceae	1

SHRUBS <5m

GENUS	SPECIES	AUTHORITY	FAMILY	DI
Bambusa	sp.		Poaceae	3
***** Chromolaena	odorata	(L.) King & Robinson	Asteraceae	3
Clerodendrum	japonicum	(Thunb.) Sweet	Verbenaceae	3
***** Clidemia	hirta	(L.) D. Don	Melastomataceae	3
Cordia	macrostachya	Roem & Schlucht.	Boraginaceae	3
Desmanthus	virgatus	(L.) Willd.	Mimosaceae	3
Homalanthus	populifolius	Graham	Euphorbiaceae	3
Ipomoea	fistulosa	Mart. ex Choisy	Convolvulaceae	3
Jatropha	curcas	L.	Euphorbiaceae	3
Jatropha	gossypiifolia	L.	Euphorbiaceae	3
***** Lantana	camara	L.	Verbenaceae	3
Melastoma	malabathricum	L.	Melastomataceae	3
Pluchea	odorata	(L.) Cass.	Asteraceae	3
Rhodomyrtus	tomentosa	(Ait.) Hassk.	Myrtaceae	3
Rubus	alcaefolius	Poir.	Rosaceae	3
Rubus	argutus	Link	Rosaceae	3
Rubus	moluccanus	L.	Rosaceae	3
Rubus	rosifolius	Sm.	Rosaceae	3
Solanum	torvum	Sw.	Solanaceae	3
***** Ulex	europaeus	L.	Papilionaceae	3
Wikstroemia	indica	(L.) C.A. Meyer	Thymeliaceae	3
Acacia	farnesiana	(L.) Willd.	Mimosaceae	2
Atriplex	lentiformis	(Torr.) S. Wats.	Chenopodiaceae	2
Bocconia	frutescens	L.	Papaveraceae	2
Buddleja	asiatica	Lour.	Buddlejaceae	2
Carica	pubescens	Lenné & K. Koch	Caricaceae	2

Citrus	medica	L.	Rutaceae	2
Clerodendrum	quadriloculare	(Blanco) Merrill.	Verbenaceae	2
Colubrina	asiatica	(L.) Brongn.	Rhamnaceae	2
Cordia	myxa	L.	Boraginaceae	2
Eugenia	uniflora	L.	Myrtaceae	2
Flacourtia	jangomas	(Lour.) Räuschel	Flacourtiaceae	2
Furcraea	hexapetala	(Jacq.) Urban	Agavaceae	2
Linoceria	intermedia	Wight	Oleaceae	2
Melastoma	decifidium	Roxburgh	Melastomataceae	2
Mimosa	acantholoba	(Willd.) Poir.	Mimosaceae	2
Piper	adancum	L.	Piperaceae	2
Pluchea	indica	(L.) Less.	Asteraceae	2
Punica	granatum	L.	Lythraceae	2
Rubus	ellipticus	Smith	Rosaceae	2
Rubus	glaucus	Bth.	Rosaceae	2
Rubus	sp.		Rosaceae	2
Senna	alata	(L.) Roxb.	Caesalpiniaceae	2
Senna	didymobotrya	(Fresen.) H. Irwin & Barneby	Caesalpiniaceae	2
Spiraea	cantoniensis	Lour.	Rosaceae	2
Triphasia	trifolia	(Burm. f.) P. Wilson	Rutaceae	2
Ardisia	crenata	Sims	Myrsinaceae	1
Ardisia	crispa	(Thunb.) A.DC.	Myrsinaceae	1
Cassia	auriculata	L.	Caesalpiniaceae	1
Elaeagnus	umbellata	Thunb.	Elaeagnaceae	1
Fuchsia	boliviana	Carr.	Onagraceae	1
Glycosmis	parviflora	(Sims) Little	Rutaceae	1
Indigofera	suffruticosa	P. Miller	Papilionaceae	1
Rubus	niveus	Thunb.	Rosaceae	1
Rubus	racemosus	Roxb.	Rosaceae	1
Tephrosia	candida	DC	Papilionaceae	1

SUB-SHRUBS some parts somewhat woody

GENUS	SPECIES	AUTHORITY	FAMILY	DI
Ageratina	adenophora	(Sprengel) King & Robinson	Asteraceae	3
Mimosa	invisa	C. Martius	Mimosaceae	3
Sida	acuta	Burm. f.	Malvaceae	3
Gossypium	hirsutum	L.	Malvaceae	2
Ricinus	communis	L.	Euphorbiaceae	2

VINES

GENUS	SPECIES	AUTHORITY	FAMILY	DI
Caesalpinia	decapetala	(Roth) Alston	Caesalpiniaceae	3
Cardiospermum	halicacabum	L.	Sapindaceae	3
Cryptostegia	grandiflora	R.Br.	Asclepiadaceae	3
Ipomoea	carnea spp fistulosa	(Martius ex. Choisy) Austin	Convolvulaceae	3
Lonicera	japonica	Thunb.	Caprifoliaceae	3
***** Passiflora	mollissima	(H.B.K.) Bailey	Passifloraceae	3
Passiflora	suberosa	L.	Passifloraceae	3
Anredera	cordifolia	(Ten.) Steenis	Basellaceae	2
Aristolochia	littoralis	Parodi	Aristolochiaceae	2
Hedera	helix	L.	Araliaceae	2
Hiptage	benghalensis	(L.) Kurz	Malpighiaceae	2
Merremia	tuberosa	(L.) Rendle	Convolvulaceae	2
Mikania	scandens	(L.) Willd.	Asteraceae	2
Passiflora	edulis	Sims	Passifloraceae	2
Passiflora	ligularis	Juss.	Passifloraceae	2
Derris	elliptica	(Wallich) Benth.	Mimosaceae	1
Thunbergia	alata	Boj. ex Sims	Acanthaceae	1
Thunbergia	grandiflora	Roxb.	Acanthaceae	1

HOW REPRESENTATIVE IS THE INVASIVE WOODY PLANT DATABASE?

Although the data presented in this report are preliminary and therefore not comprehensive it was difficult to estimate how representative the dataset is. When the report was near completion a search of Forestry Abstracts for 1995 yielded a reference of a report on naturalized exotic tree species in Puerto Rico by Francis & Liogier (1991). The authors list and rate the invasive potential of 118 introduced tree species. This information could not be included in the database but can be used to estimate the coverage of the Invasive Woody Plant Database. Out of Francis and Liogier's 118 species only 42% are included in the database and two (1.7%) are recorded as invasive in Puerto Rico. They identified 16 species as widespread and competing in primary and secondary forests and a second group of 16 species able to regenerate and spread in forests which they forecast as becoming common or abundant within 100 years. The respective percentage of species not held in the database are 31% and 58%. Highly and moderately invasive species in Puerto Rico not held in the database and not found in Table 5.1 are listed in Table 4.1. The percentage of possibly/potentially, moderately and highly invasive species is 72%, 14% and 14% respectively. The relative proportion of these three groups of invasive species in Puerto Rico is markedly different from the database figures of 16%, 60% and 24% (Table 8) indicating that possibly/potentially invaders are under reported.

Table 4.1. Invasive woody plants reported by Francis & Liogier (1991) not found in the Invasive Woody Plant Database.

"Species common or abundant, widespread, and competing in primary or secondary forests stands"	"Species that have been able to regenerate and compete in forests stands and are likely to become common or abundant within the next century"
Ardisia solanaceae Roxb.	*Albizia adinocephala* (D.Donn. Sm.) Britt & Rose
Artocarpus altilis (S.Park.) Fosb.	*Castilla elastica* Cerv.
Muntingia calabura L.	*Haematoxylon campechianum* L.
Senna siamea (Lam.) Irwin & Barnaby	*Hibiscus elatus* Sw.
Thespesia populnea (L.) Soland ex Correa	*Lysiloma latisiliqua* (L.) Benth.
	Mimosa arenosa (Willd.) Poir
	Pterocarpus macrocarpus Kuez
	Senna mutijuga (L.C. Rich.) Irwin & Barneby
	Senna spectabilis (L.C. Rich.) Irwin & Barneby
	Simaboura amara Aubl.
	Sterculia apetala (Jacq.) Karst.

5 CASE HISTORIES OF HIGHLY INVASIVE WOODY SPECIES IN THE TROPICS

5.1 INTRODUCTION

The Invasive Woody Plant Database, like any ecological database, can be used to provide an overview of invasion by woody plant species as presented in the previous section. However, information on a ecological database cannot provide a comprehensive picture of the complex interactions of ecological, environmental and historical factors affecting plant invasions. Here, to provide further insight into the subject we present a series of case histories of woody plant invasions. Due to the limited number of well investigated cases only a small subset of the species found in the Invasive Woody Plant Database can be reported in detail.

Cronk & Fuller (1995) give detailed accounts on six species dealt with here, namely *Clidemia hirta*, *Lantana camara*, *Melaleuca quinquenervia*, *Mimosa pigra*, *Passiflora mollissima* and *Pittoporum undulatum* as well as another tropical woody plant *Psidium cattleianum*. Cronk & Fuller have used a different approach to produce their account focusing more on the control and management of the species, botanical description as well as reported cases of introductions and invasions.

In Australia, substential accounts of *Acacia nilotica* (Mackey 1996a), *Cryptostegia grandiflora* (Mackey 1996b), *Prosopis* spp. (Csurhes 1996) and *Senna obtusifolia* (Mackey *et al.* 1997), with special refrence to Queensland, have been produced. The Department of Primary Industry and Fisheries of the Northern Territory publishes 'Agnote' which consists in a large number of short accounts on weeds of the Northern Territory and include a number of invasive woody plants (e.g. *Prosopis limensis* (Gracie 1992), *Mimosa pigra* (Smith & Miller 1991)).

Other useful species accounts may be found in Anon. (1980, 1983) and Holm *et al*. (1977).

A number of Web sites have species accounts and the relavant ones are:

Cryptostegia grandiflora: http://leaky.rock.tap.csiro.au/facts/woody.html#Rubbervine

Parkinsonia aculeata: http://leaky.rock.tap.csiro.au/facts/woody.html#Parkinsonia

Zizyphus mauritiana: http://leaky.rock.tap.csiro.au/facts/woody.html#Chinee

Invasives in Hawaii: http://www.botany.hawaii.edu/faculty/cw_smith/aliens.htm

5.2 SPECIES DESCRIPTIONS

In each species account information on a number of species attributes and on various environmental and ecological characteristics of the native and invaded ranges is reported. Each account is divided into five main sections and the details are given below. Wherever necessary, assumptions made, limitations to information supplied and required explanations are indicated.

Species characteristics

- Synonyms of botanical names are included only if they have been used in TREE-CD over the past five years.
- Life form, size, lifespan
- Taxonomy, variation and plasticity
- Reproductive biology
- Resilience and resistance
- **This section focuses on the species ability to respond to physical damage, fire, drought, flooding, pests and diseases**
- Environmental requirements and successional status
- Products and uses

Status in native range

- Range and abundance
- Climate
- Site requirements
- Weediness
- Pests and diseases

Status in invaded regions

In this section all information given refers to the most highly invaded region unless stated otherwise
History of introductions and intensity of invasions
Patterns of invasion and time-lag
Site and climate
Floristic region and vegetation types
Pests and diseases
Impact on ecosystem
Impact on humans and related activities
Control

Ecological differences

Existence of ecologically equivalent species and competitive interactions in invaded regions

Ecologically equivalent species should exhibit great similarities in species attributes (e.g. lifeform, size, lifespan, fruit type, dispersal agent), in site and climatic requirements as well as in successional status. Only detailed investigations can differentiate ecologically equivalent species. A good example is provided by the two European timber trees *Acer pseudoplatanus* L. and *Fraxinus excelsior* L. which differ mainly in terms of duration in seed dormancy, tolerance to flooding, susceptibility to grass competition and variation in latitudinal and altitudinal distributions (Binggeli 1992). Another example is the case of *Quercus robur* L. and *Q. rubra* L., the latter invading forests dominated by the former, reported by Barkman (1988).

Differences in status and ecology between invaded and native ranges

Selected references

Up-to date key references on the ecology of a species in its native and invaded ranges as well as key references on other subjects such as botanical description, taxonomic treatment, species bibliographies, diseases and biological control are given. Each reference is annotated as follows: * reference on invasion, ** key reference on invasion; • reference on native range, •• key reference on native range; # references on other subjects relating to the species including: botanical description, pest and diseases, reviews etc...

5.3 SPECIES ACCOUNTS

The species accounts of 18 tropical invasive woody plant are available and are listed in Table 5.1.

Table 5.1. Woody plant species for which a detailed account is available (S = shrub, sT = small tree, T = tree and V = vine).

SPECIES	FAMILY	LF	Native region	Invaded regions	Habitat invaded
Acacia nilotica	Mimosaceae	T	Africa-India	Australia, Indonesia	grassland
Casuarina equisetifolia	Casuarinaceae	T	Australasia	Florida	coastal sands
Cecropia peltata	Cecropiaceae	T	neotropics	Africa, Asia	disturbed areas, forest gap
Chromolaena odorata	Asteraceae	S	neotropics	Africa, Asia	fallow, logged forest
Clidemia hirta	Melastomataceae	S	neotropics	Oceanic islands	disturbed areas, forest
Lantana camara	Verbenaceae	S	neotropics	tropics	pasture, plantations
Leucaena leucocephala	Mimosaceae	sT	C. America	Pacific islands	disturbed areas
Maesopsis eminii	Rhamnaceae	T	Africa	East Africa	natural & secondary forest
Melaleuca quinquenervia	Myrtaceae	T	Australia	Florida	swamp
Miconia calvescens	Melastomataceae	sT	neotropics	Pacific islands	forest
Mimosa pigra	Mimosaceae	sT	neotropics	Australia, Thailand	flood plain
Myrica faya	Myricaceae	sT	Atlantic Isl.	Hawaii	lava flows
Passiflora mollissima	Passifloraceae	V	neotropics	Hawaii	forest
Pinus patula	Pinaceae	T	Mexico	East Africa	forest, grassland
Pittosporum undulatum	Pittosporaceae	T	Australia	Jamaica	forest
Psidium guajava	Myrtaceae	sT	neotropics	Pacific islands	pasture, forest
Schinus terebinthifolius	Anacardiaceae	sT	S. America	Florida	disturbed areas, grassland
Ulex europaeus	Papilionaceae	S	W. Europe	mountain tropics	pasture

Acacia nilotica (L.) Del. (Mimosaceae)

A. arabica (Lam.) Willd.

A variable and widely used tree from Africa and the Indian subcontinent. Subsp. *indica*, introduced to northern Australia, has spread into dry grassland, slowly at first, but then with population explosions during wet years.

Species characteristics

Life form, size, lifespan

Thorny small tree growing to a height of 7 m. Lives at least 60 years.

Taxonomy, variation and plasticity

Nine sub-species are recognised. Hybridization between the various ssp. occurs and has been influenced by human's seed dispersal. Within the *A. nilotica* complex the pods are very variable.

Reproductive biology

The yellow sweetly scented flowers are nectarless and found in round heads. Most flowers are functionally male with a few hermaphrodites and are mainly bee-pollinated. Pods are indehiscent. Seed production is high (up to 175,000 seeds/tree) and yearly provided water is plentiful like along water courses. In Kenya seed set per pod was 10.8 and trees produced between 153 and 34,000 seeds. It forms large seedbanks and in Australia the half-life of seeds is 10-12 months.

Leaf production and fall are affected by rainfall whereas temperature affect flowering and fruiting. In Sudan *A. nilotica* flowers irregularly but generally between June and September and seed fall takes place from march to May. In Australia trees flower from March to June and green pods are produced within four months but ripe pods fall from November to February. Most of the leaf fall occurs during the dry period when the tree bears green pods.

Resilience and resistance

Species is sensitive to frost but is tolerant of grazing, drought (< 2 years), fire and salinity.

Environmental requirements and successional status

Requires water for seed germination and seedling establishment. Can regenerate under pioneer woody plants in seasonally flooding habitats and subsequently outcompete them.

Products and uses

Extensively used as browse, firewood and timber. The bark and seeds are a source of tannin while bark, roots and flowers are used for medicinal properties. The gum is sometimes used. The wood is suitable for paper production. Planted for forestry or reclamation of degraded land.

Status in native range

Range and abundance

Native to India, Pakistan and much of Africa where it is often dominant.

Climate

Grows in areas where the mean monthly temperature of the coldest month is above 16℃. It tolerates a wide range of rainfall from less than 350 mm to more than 1500 mm or more per year.

Site requirements

A. nilotica subsp. *indica* is commonly found on soils with a high clay content, but in areas of higher rainfall it may grow on deep sandy loam. Often found growing close to waterways on seasonally flooded river flats. In Sudan, along the Nile, regeneration has been reported as occurring once every ca. 15 years following high floods.

Weediness

With the exception of *A. nilotica* spp. *kraussiana* in southern Africa, there does not appear to be much evidence to show that the tree is weedy in its native range.

Pests and diseases

Many wild mammals feed on seed pods and a large number of insect species attack the mature seed.

Status in invaded regions

History of introductions and intensity of invasions

A. nilotica subsp. *indica*, native to the region spanning from Ethiopia to Burma, was introduced to Iran, Vietnam, the Caribbean and Australia. Introduced to Australia around 1900 as a shade tree along bore drains in Queensland. Found elsewhere in Australia but the distribution is limited by frost. Around 1960 it was found in 7% of the Mitchell grassland areas and by the mid 1980s it covered 6.6 million ha or 25% of the area. Its distribution and population densities are still increasing. Since 1969 introduced to the Baluran National Park (Java, Indonesia) as a firebreak and is spreading vigorously.

Patterns of invasion and time-lag

Dramatic increase in *A. nilotica*, particularly on town commons, took place in the 1950s as a result of a series of years with above average rainfall. Following this population outbreak the species was declared a noxious weed. Instead or removing the plant as required, many landholders continued to plant them along open drains distributing artesian water. The constant water supply ensured fast grow rates and the production of large seed crops, which were spread by cattle throughout the surrounding countryside forming large seedbanks. During a second period of above average rainfall in the mid-1970s germination of the seedbank occurred and resulted in a 1000 fold increase in *A. nilotica* populations. The highest densities of *A. nilotica* are found on properties which had the tree planted along its drains prior to the 1970s and had cattle rather than sheep grazing. In the 1980s a prolonged drought has reduced tree density in some areas by up to 80%. In Indonesia it invaded, with apparently no time-lag, wild grasslands.

Site and climate
Clay soils in dry tropics.

Floristic region and vegetation types
In northern Australia, *A. nilotica* is spreading into grassland dominated by *Astrebla* spp.

Pests and diseases
Two insect species, including one Coleoptera introduced as an attempt at biological control, eat the seeds unless they are quickly ingested by mammals soon after ripening. The passage through the digestive track of cattle apparently make seeds nearly immune to insect attack.

Impact on ecosystem
The vast grasslands of northern Australia are changed into woodland. In Indonesia it is altering the physiognomy of the invaded ecosystem and depriving native mammals of grazing grounds.

Impact on humans and related activities
The invasion reduces the livestock carrying capacity of Queensland's Mitchell grasslands. It may have an impact on the number of tourists frequenting the Baluran National Park as most visit the park to view large herds of herbivores.

Control
In Indonesia both mechanical and chemical control have been practised and the former was found to be more economical. In Australia a biological control programme has been initiated.

Ecological differences

Existence of ecological equivalent species and competitive interactions in invaded regions
The invaded ecosystem is grassland and therefore is treeless. This is an example of a lifeform hitherto absent being able to spread.

Differences in status and ecology between invaded and native ranges
A. nilotica appears to suffer from fewer insect pests, particularly seed pests, in Australia than in native range.

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Pierre Binggeli

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Casuarina equisetifolia L. (Casuarinaceae)

Drought and salt resistant tree from Australasia widely planted in the tropics and sub-tropics. In Florida it is spreading on sandy shores and in areas disturbed by hurricanes. It forms dense stands and destroys reptiles breeding sites.

Species characteristics

Life form, size, lifespan

Evergreen tree reaching a height of 30-40 m.

Taxonomy, variation and plasticity

The var. *equisetifolia* and var. *incana* Benth. differ in height and stem straightness the latter being smaller and a poorer stem form and a more open canopy. Many morphological features are very variable.

Reproductive biology

The species is monoecious or dioecious with 2-3% of the individuals being monoecious. Males start to flower in the second year whereas females one year later. wind pollinated. The fruit is like a woody cone, 1 to 2 cm in diameter. They contain 70-90 seeds and take 3-4 months to mature. The seeds (achenes: 600 to 2000 seeds per g) have a membranous wing and are wind-dispersed. They can also be water-dispersed. Germination rate varies between 30 and 84 % but seeds are only viable for a few months. Usually, there are two main flowering and fruiting seasons although some fruits are often produced all year round, but in Hawaii and Puerto Rico flowering and fruiting are irregular. Seeds are produced annually.

Resilience and resistance

Adaptations to dry climate include scale-light verticillate leaves and modified needle-like twigs for reducing transpiration by means of sunken stomata lying in grooves, hairs, thickened cells and cuticle. Roots have nodules with symbiotic nitrogen fixing bacteria. It is not resistant to frost and has low fire tolerance but is salt tolerant. Adapted to growth on sand dunes as lower branches root and upright branches develop. Stilt roots and prop roots are sometimes in waterlogged areas. Does not suffer from browsing. When cut the tree sprouts profusely. It is often propagated by cuttings and in India by layering from low spreading branches.

Environmental requirements and successional status

A light demanding species which needs open sites for establishment, free from plant competition. It forms permanent stands in saline coastal environments and sand dunes.

Products and uses

The strong and heavy wood is durable in the ground and submerged in saltwater. It is a very good firewood and fine for charcoal whereas it is not adequate for fine carpentry. Widely planted for amenity purposes, coastal reclamation, medicinal purposes, tannin, dyes, pulp and timber.

Status in native range

Range and abundance

Native to Australasia. In Australia the var. *equisetifolia* occurs along a narrow coastal strip of tropical Australia whereas var. incana extends south (to 32°S). Altitudinal range: sea level to 100 m.

Climate

Var. *equisetifolia* occurs in the hot humid and sub-humid zone (monsoonal) whilst var. *incana* is found in the warm sub-humid zone. Frost occasionally occur inland in the most southern part of var. *incana* range. Typical rainfall lies between 1000 and 1500 mm a year.

Site requirements

Found in dry and exposed habitats, typically coastal sand dunes. Var. *incana* may also occur around the bases of rocky headlands. Usually it is the only woody plant in vegetation dominated by grasses and herbs. Sometimes found associated with eucalypts.

Weediness

Not recorded.

Pests and diseases

Seeds are carried off in large quantities by ants. Seeds and seedlings are attacked by insects and crabs. It suffers from many fungal diseases.

Status in invaded regions

History of introductions and intensity of invasions

In Florida, var. *incana* Benth., was introduced around 1900 and planted by farmers and fishermen near homesteads and citrus groves for shade or as windbreak. In the 1930s trees planted to reclaim swampland as it was erroneously thought that the trees would dry the swamps. Extensively planted for reforestation in many parts of the world mostly on coastal dunes as well as in new urban areas of Malaysia. It was introduced to India as early as the 1860s but its provenance is unknown.

Patterns of invasion and time-lag

C. equisetifolia first started to spread along shell beaches and open sands, and by the 1950s it was only found in scattered locations in the Everglades National Park. Two successive hurricanes in 1960 and 1965 created the disturbed areas necessary for the rapid spread of *C. equisetifolia*. The species didn't survive well in areas of prolonged flooding and its spread inland was restricted by fire.

Often found in nitrogen deficient soils in urban areas where the top-soil has been removed. For instance, with *Acacia auriculaeformis,* it dominates the pioneer vegetation in urban areas of Malaya.

Site and climate

Floristic region and vegetation types

Coastal herbaceous swamp and broad-leaved hammock communities.

Pests and diseases

In Malaya it does not appear to suffer from pests although it harbours *Icerya purchasi,* a pest of orange and lemon. Many pathogens threaten extensive plantations in many parts of the world. In India a stem borer kills shoots and seedling damping-off by *Rhizoctonia* spp. occurs in nurseries. In Puerto Rico natural regeneration is rare because ants eat nearly all the seeds.

Impact on ecosystem

In Florida its roots can prevent turtles from digging nests for their eggs, and sometimes turtles are trapped by the roots. On coastal areas subject to wave erosion, toppled trees act as groynes, increasing loss of sand. Under the dense shade cast by *C. equisetifolia* canopy a thick mat of twigs is formed which prevents regeneration.

Impact on humans and related activities

The large quantities of air-borne pollen cause respiratory irritations. In Florida this large tree (up to 30 m) is considered as a public safety hazard. During hurricanes the fall of *C. equisetifolia* can damage property or block evacuation roads. In northern areas frost-killed trees become a nuisance due to the fall of branches and crowns. It often forms dense stands which are nearly impossible to walk through.

Control

Its threat to the Everglades National Park was quickly realised and a control programme was initiated. Seedlings were easily uprooted and larger trees killed by cutting or girdling and treated with the herbicides. However, the herbicides used in the 1960s, 2,4,5-T and 2,4-D, were and other herbicides have since been used with limited success. The spread of the species had been contained by the early 1980s but as seeds are continuously brought in from mature stands inside and outside the park, continuing seedling control is required. At present resources are not available to deal with the large dense stands.

Ecological differences

Existence of ecological equivalent species and competitive interactions in invaded regions

C. equisetifolia invades coastal areas of Florida which are free of woody plant species.

Differences in status and ecology between invaded and native ranges

No obvious differences are apparent, although no diseases have been reported from Florida suggesting that they have little impact on the invading population.

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Pierre Binggeli

May 1997

Cecropia peltata L. (Cecropiaceae)

Short-lived light demanding tree from tropical America introduced to African and Malaysian botanical gardens or as a shade tree in Ivory Coast. Spreading in disturbed areas, lava flows and forest gaps without displacing native equivalents.

Species characteristics

Life form, size, lifespan

Tree to 20 m high with a lifespan of 20-30 years. It has large leaves and a small crown.

Taxonomy, variation and plasticity

The current work on the taxonomy of the genus *Cecropia* suggest that *C. peltata* L. (central America), *C. pachystachya* Trécul (southern America) and *C. concolor* Willd (Amazon basin) should be regarded as part of the *C. peltata* complex as they have strong morphological similarities (specimen of unknown origin can not be adequately defined) but have somewhat distinct geographical and/or ecological ranges. Usually evergreen but may be deciduous in areas with a pronounced dry season.

Reproductive biology

C. peltata is dioecious and becomes sexually mature in 3 to 5 years. The minute flowers are clustered on 5 to 10 cm long spikes and are wind-pollinated. On female individuals the minute one-seeded fruits form large fruit clusters which appear to take around a month to mature. A spike contains around 800 viable seeds which are about 1.9 mm long and weigh 1.6 mg. In Trinidad bats eat large quantities of the succulent fruits, thus are the main seed disperser although birds also distribute the seeds. In Costa Rica a similar amount of fruits are consumed during the day, mainly by monkeys, and at night by bats and arboreal mammals. A large and persistent seedbank is formed in the forest soil. In Costa Rica flowering and fruiting are seasonal lasting about 9 months with a peak of 4 months during the early part of the wet season.

Resilience and resistance

In most of its native range *C. peltata* is inhabited by stinging ants which were thought to protect the tree from herbivory, however in Puerto Rico, where ants are not associated with the species, trees thrive. *C. peltata* coppices freely following cutting.

Environmental requirements and successional status

Shade intolerant species which dominates early succession.

Products and uses

The light wood variously used for matchsticks, boxes and crates, interior boarding and paper pulp. Hollow branches and trunks are used to make floats, gutters and trumpets. In places the leaves, latex or bark are employed in medicinal remedies.

Status in native range

Range and abundance

The three sub-species of the *C. peltata* complex are distributed as follows: *C. peltata* in Central America, northern South America and some Caribbean islands, *C. pachystachya* from central and eastern Brazil to northern Argentina and *C. concolor* in the Amazon basin. In Puerto Rico *C. peltata* is one of the most abundant trees. In many parts of its range the species abundance has increased following human related disturbance. In natural forests it is common but patchily distributed.

Climate

Moist tropical and sub-tropical regions, but is absent from dry coastal and dry limestone areas.

Site requirements

Regenerates freely as soon as open areas are formed. In natural forests it only becomes established in large gaps and often fails to reach sexual maturity in gaps <150 m2.

Weediness

It is abundant in open areas and in logged and natural forests throughout Puerto Rico and is generally considered to be a weed tree.

Pests and diseases

It is attacked by *Historis* spp. and various moth species.

Status in invaded regions

History of introductions and intensity of invasions

The tree was introduced to a number of botanical gardens in Cameroon (Limbe formerly Victoria: early 20th century), Zaire (Eala, 1911) and Java (Bogor). In 1953 a trial plot was set up in Malaysia using seeds from Bogor and the species was introduced to Ivory Coast in 1910 as a shade tree in coffee plantations. In 1953 trial plantations were set up in Malaysia. Since the Eala and Bogor material originated from Brazil they would therefore appear to be *C. pachystachya*, whereas the identity of the Cameroon and Ivory Coast plants is unclear as their origin is unknown.

Patterns of invasion and time-lag

In the three African regions where *C. peltata* was introduced, the species has been spreading in disturbed areas in competition with native 'pioneer' species. In Cameroon *C. peltata* has spread into the gaps of a natural forests where its native equivalent *Musanga cecropioides* is still 2.5% more common. It has also been recorded as colonizing old lava flows on Mt Cameroon. Along roadsides pure stands may be encountered. In most regions the tree started to spread soon after the introduction. However, in the Ivory Coast the rate of spread was very slow for the first six decades and only after the destruction of most the forest cover did the speed of its spread increase markedly.

Site and climate
Lowland disturbed forests or deforested areas in moist tropical areas. Climate is often seasonal.

Floristic region and vegetation types
Found in a variety of floristic regions.

Pests and diseases
Sometimes the tree is extensively defoliated in Cameroon.

Impact on ecosystem
Competes with or appear to displace native pioneer trees. Impact on vegetation succession unknown.

Impact on humans and related activities
No reports have been made. The tree would probably be regarded as another weedy species without any particularly obnoxious features.

Control
Control of *C. peltata* has not been reported.

Ecological differences

Existence of ecological equivalent species and competitive interactions in invaded regions
In tropical Africa *C. peltata* appear to be displacing or at least competing with an ecologically equivalent tree *Musanga cecropioides* R. Br. ex Tedlie. Both trees are taxonomically related and morphologically similar. *C. peltata* appears to grow faster and is more commonly found on exhausted agricultural soils. Under greenhouse conditions seed germination of the native species is much harder to achieve than that of the exotic. In Malaysia native pioneer species regenerate in smaller forest gaps, produce larger seeds, grow slower in full sunlight and suffer from higher leaf loss rates than *C. peltata*.

Differences in status and ecology between invaded and native ranges
No obvious differences between the successional status, habitat requirements or susceptibility to herbivores between the native and invaded regions are noticeable.

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Pierre Binggeli

September 1999

Chromolaena odorata (L.) King & Robinson (Asteraceae)

Eupatorium odoratum L.

A widely distributed neotropical shrub introduced to many parts of the tropics. Forms pure stands in disturbed areas, grasslands, fallows and forestry plantations. Species spreading rapidly due to its efficient short- and long-distance dispersal abilities.

Species characteristics

Life form, size, lifespan
Multi-stemmed shrub to 2.5 m tall in the open and to 10 m tall when climbing vegetation.

Taxonomy, variation and plasticity
The invasive populations of *C. odorata* in Asia and southern Africa, both originating from the Caribbean, are morphologically different.

Reproductive biology
Sexual reproduction starts when the plants is one year old. Terminal cymes bear around 70 insect-pollinated flowers. The small fruits (weight: 0.2 mg) mature in about a month. A dense thicket of *C. odorata* may produce about 109 seeds ha-1 in Ivory Coast and has a very large seedbank. Fruits (cypsella) are typically wind-dispersed as dry and windy weather is necessary for fruit release, however animal dispersal is possible thanks to the fruits small hooks. Flowering initiation appear to be mainly related to the onset of the main dry season and last for three to five months. Seed germination is favoured by water and light and therefore takes place at the start of the rainy season. In India seed dispersal and germination occur before (April-May) and at the start (May-June) of the rains respectively. Active growth takes place through the rainy period until October and is followed by flowering. Seed reach maturity in March.

Resilience and resistance
Shoots may root when touching the ground. It possess an underground 'organ' which ensure the plant's survival in case of fire, drought or mechanical damage through coppicing.

Environmental requirements and successional status
Frost intolerant and is adverse to dry regions. Flourishes in disturbed habitats, particularly in areas of slash an burn agriculture. In Trinidad (native range) on open land *C. odorata* is a successional species which supersedes the pioneer ephemeral herbs, then is displaced by shrubs and small trees and dies as soon as the forest canopy closes.

Products and uses
Ornamental plant appreciated for its winter flowers. In the West Indies it is known as the 'Christmas bush'. Formerly thought to be useful in controlling coarse grasses, mainly *Imperata* spp.

Status in native range

Range and abundance
Wide distribution in the neotropics from the USA (29o N) to Argentina (31o S) including most of the West Indian islands.

Climate
Tolerates a variety of temperate and tropical climates. In South America on the western side of the Andes the species does not spread south of 7o S as the conditions are to dry.

Site requirements
Grows from sea level to 1000 to 2800 m. It occurs on open freely-drained grounds and is absent in natural forests.

Weediness
Site density appears to have increased since last century as a result of human's impact on the environment.

Pests and diseases
Over 240 arthropods have been recorded *on C. odorata* in Trinidad where the species was investigated in detail for potential biocontrol agents.

Status in invaded regions

History of introductions and intensity of invasions
Introduced to botanical gardens of Dacca (India), Java and Peradeniya (Sri Lanka) in the 19th century and for ornamental reasons in Southern Africa early 20th century. In Western Africa the plant was accidentally introduced with forestry seeds in Nigeria in 1947 and was deliberately introduced to Ivory Coast in 1952 to control *Imperata* spp. following a recommendations by the famous botanist Auguste Chevalier. In 1994 small infestations of *C. odorata* were found in Queensland, Australia and it is suspected that the introduction resulted from contaminated pasture seeds from overseas. Introduced and spreading on a number of tropical islands and is also found in a number of temperate regions.

Patterns of invasion and time-lag
In Indian fallows *C. odorata* recruitment peaks after 3 years and ceases in 10 to 20 years old fallows.

Seedling mortality is higher in older fallows and plant vigour decreases after 5 years. Thus the duration of fallows will greatly affect the local abundance of *C. odorata*. Elsewhere in India in established vegetation *C. odorata*'s survivorship was only 1.4 % in the first year's cohort but much higher in older individuals. Still, despite the high mortality this resulted in a 30% increase in population size in one year. In an Indian monsoon forest *C. odorata* regenerated freely in selection-felling gaps but was absent from treefall gaps in undisturbed forest. In slash and burn rice cultivation in Ivory Coast forests the fields, if cultivated for only one year, will quickly be filled with pioneer trees after abandonment whereas after 3 years *C. odorata* will become dominant. Most seed dispersal is local, however, as the seeds have small spines and can cling to fur, feathers and clothes, long distance dispersal is possible. Seeds can also travel great distances with contaminated crop plants or vehicles. In Australia dispersal appear to have also included water, cattle, horses, feral pigs and sugar cane harvesting equipment. No time-lag has been reported.

Site and climate
Distribution limited by rainfall but no absolute minimum exist. The species is generally not present in areas with <1200 mm of rainfall a year and occurs predominantly at altitudes below 1000 m. The species does not appear to have special soil requirements.

Floristic region and vegetation types
Associated with local weeds or secondary vegetation of disturbed areas.

Pests and diseases
In Ivory Coast only insects feed on *C. odorata* with little impact on the species.

Impact on ecosystem
In Western Africa *C. odorata* suppresses regeneration of tree species in areas of shifting cultivation if its become well-established. In southern Africa it reduces species diversity and the plants flammability poses a threat to forest edges.

Impact on humans and related activities
C. odorata is a problem in agricultural land and commercial plantations.

Control
In several tropical countries biological control, using a defoliating artiid, was initiated in the early 1970s generally without success at the exception of Sri Lanka and in the 1980s of Guam. To date only one species has been tried for biological control. An eradication programme has been initiated in Australia using herbicide.

Ecological differences

Existence of ecological equivalent species and competitive interactions in invaded regions
Grows faster than native pioneer species in Ivory Coast.

Differences in status and ecology between invaded and native ranges
Apart from the apparent higher pest problem in the native range no evidence is available.

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Pierre Binggeli

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Clidemia hirta (L.) D. Don (Melastomataceae)

Neotropical bird-dispersed shrub introduced to many parts of the tropics. Considered a weed on many oceanic islands where it forms dense thickets and suppresses most ground vegetation. Even small stands are impossible to eradicate.

Species characteristics

Life form, size, lifespan

Densely-branched shrub up to 5 m tall but normally between 0.5 and 3 m.

Taxonomy, variation and plasticity

A taxonomically difficult genus and the plant has sometimes been misidentified. Varieties of *C. hirta* have been described. Var. *hirta* and var. *elegans* were introduced to Hawai'i and the Seychelles respectively.

Reproductive biology

Several white or pinkish flowers borne on axillary or terminal cymes. A mature plant can produce over 500 blue-black berries (6-9 mm long) per year each containing over 100 seeds (0.5-0.75 mm long). Seeds form a very large seedbank where they remain viable for up to 4 years. In Hawai'i, long distance dispersal is carried out by humans and seeds are locally-disseminated by birds and feral pigs which can also carry seeds in their fur. In Hawai'i flowering and fruiting occurs all year round where there is no dry season and rainfall exceeds 2500 mm.yr-1. In areas where a dry season occur flowering ceases.

Resilience and resistance

In windy areas the shrub is scrambling and is less than 1 m tall. Resistant to drought lasting up to 6 months although some shoot tips die back during the dry season. It does not appear to tolerate salt-spray. On the ground of rain forests detached leaves can root.

Environmental requirements and successional status

In the native range it is an early coloniser of disturbed areas and is rapidly replaced by vines. Tolerates full sun light as well as complete canopy cover.

Products and uses

Has no fodder value and no known uses.

Status in native range

Range and abundance

Widely distributed in Central and South America and the Caribbean islands where it is not a very common plant.

Climate

Broad climatic requirements ranging from dry to wet tropics.

Site requirements

It is an early colonizer of open areas, including slash-and-burn agricultural grounds, where it becomes dominant twelve months after disturbance before being smothered by vines. It is found in low densities in open forested areas, forest plantations, and roadsides. In Jamaica its altitudinal distribution ranges between 30 and 1200 m a.s.l.

Weediness

Not weedy but said to be common in Jamaica in moist pastures.

Pests and diseases

All plants show signs of heavy herbivory.

Status in invaded regions

History of introductions and intensity of invasions

C. hirta is a serious weed on many tropical oceanic islands (e.g. Fiji, Seychelles), southeast Asia, India and East Africa. The date of introduction to Hawaiian Islands is unknown and it was first recorded in 1941. It was grown in the Wahiawa Botanic Garden and was thought to be "very promising because it won't be spread by birds". It was first noted as escaping in 1949 on the island of O'ahu and by 1952 covered at least 100 ha. By the late 1990s it had invaded all suitable habitats covering over 100,000 ha. In the 1970s and 1980s it was accidentally introduced by humans to five other Hawaiian islands. On Fiji *C. hirta* was probably accidentally introduced prior to 1890 with coffee plants imported from British Guiana. It became a pest by 1920.

Patterns of invasion and time-lag

In Hawai'i all new spread occurs in disturbed areas such as roadsides and landslides and following disturbance by windstorm, pigs and fire. If seeds are present they germinate rapidly and within two years the disturbed area can become smothered. However, on the steep slopes of the Seychelles enough light reaches the ground for *C. hirta* regeneration to take place without forest canopy disturbance. Although this species is rarely recorded until it forms monotypic stands, the more recent Hawaiian introductions suggest that it starts to spread as soon as it is introduced to new suitable habitats subjected to regular disturbance.

Site and climate

C. hirta tolerates widely differing tropical climatic conditions including a wide range of rainfall (<1000 to > 2500 mm). On the Seychelles the shrub is absent from drier areas.

Floristic region and vegetation types
Most tropical island forest areas appear to be susceptible to *C. hirta* invasion regardless of their floristic composition as long as some form of disturbance affects them.

Pests and diseases
It is only affected by one insect introduced as a biocontrol agent.

Impact on ecosystem
Under heavy infestations of *C. hirta* most plant, including most mosses and liverworts normally found in shaded habitats and subcanopy species, are displaced. It is thought that the species has the potential of driving some species to extinction.

Impact on humans and related activities
In Hawai'i the plant is despised because of its dense growth. Its growth along trails and roadsides increases maintenance costs as well as reduce the aesthetic, educational and recreational value of forest lands. In Fiji it renders large areas of grazing land useless and interferes with the development of plantations (rubber, cocoa).

Control
Biological control, using the thrips *Liothrips urichi*, was initiated in Fiji in the early 1930s and much later in Hawai'i. The introduced insect seriously affect the growth of *C. hirta* in open sunny areas whereas in shaded areas (forest or frequent cloud cover) it is not effective. The only hope of controlling an invading population of *C. hirta* is to identify the problem at a very early stage and eradicate all seed-sources. In Hawai'i repeated efforts to control seedlings in expanding populations have failed.

Ecological differences

Existence of ecological equivalent species and competitive interactions in invaded regions
No ecological equivalent appears to exist.

Differences in status and ecology between invaded and native ranges
C. hirta suffers from heavier insect herbivory and subjected to strong competition from other Melastomataceae and vines in its native range. In the native range the species is purely an early successional species whereas in parts of its invaded range it can become established below forest canopy. In Hawai'i the shrub grows taller.

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Pierre Binggeli

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Lantana camara L. (Verbenaceae)

Variable shrub native to tropical America introduced to most of the tropical and sub-tropical regions. Forms extensive impenetrable thickets in disturbed areas but is also found in the understorey of open forests.

Species characteristics

Life form, size, lifespan

Two to five meter tall shrub. Erect in the open and scrambling in scrubland.

Taxonomy, variation and plasticity

L. camara is a highly variable species. It has been cultivated for over 300 years and now has hundred of cultivars and hybrids. These belong mostly to the *Lantana camara* complex. Cultivars can be distinguished morphologically (variation in: flower size, shape and colour; leaf size, hairiness and colour; stem thorniness), physiologically (variation in: growth rates, toxicity to livestock) and by their chromosome number and DNA content.

Reproductive biology

Flowers are yellow, later turning orange then red and remain on the axillary inflorescence for three days. The flowers, when yellow, produce nectar and are pollinated by butterflies. The species is an obligate outcrosser. It is unclear whether apomixis occur. The fleshy drupe is 3-6 mm in diameter containing 1-2 seeds (1.5 mm long). Fruits mature rapidly and change colour from dark green to black. A number of bird species and sometimes sheep and goats disperse the seeds. Flowering and fruiting throughout the year with a peak during the first two months of the rainy season. Heavy fruit production produced yearly.

Resilience and resistance

The alkaloid rich leaves are virtually immune to herbivory. It can spread vegetatively. Stems and roots coppice freely following herbicidal treatment. Slashing and burning stimulate suckering. Allelopathic effect induced by *L. camara* inhibits growth of other vegetation as well as seed germination. It has low tolerance for boggy soils, saline soils and is susceptible to frost.

Environmental requirements and successional status

Thrives in open and disturbed areas as well as in open natural vegetation. Being somewhat shade-tolerant and it can become the dominant understorey shrub in open forests.

Products and uses

Ornamental plant which was often used for hedges and erosion control. Twigs are used as fuel. A number of minor uses include seeds as lamb food, biogas production when its straw is mixed with dung, and medicinal purposes.

Status in native range

Range and abundance

Native to Central and South America. Original distribution unclear due to the introduction of a number of ornamental varieties. Species poorly investigated.

Climate

Site requirements

In the West Indies it is found in dry thickets.

Weediness

In Central America *L. camara* is a weed in a number of crops and is common in pastures, waste areas and roadsides.

Pests and diseases

Many insect species attack flowers, flower stalks, leaves, stems, shoots and roots. Their impact on shrub vigour and seed set is not known.

Status in invaded regions

History of introductions and intensity of invasions

L. camara has been introduced throughout the tropics and subtropics as an ornamental, often used as a hedge plant. It is regarded as a cosmopolitan weed and in many countries it has been declared a noxious weed. Mostly introduced during the late 19th century but a number of cultivars and forms were subsequently introduced.

Patterns of invasion and time-lag

L. camara forms extensive, dense and impenetrable thickets in forestry plantations, orchards, pasture land, waste land and in natural areas. The rapid spread of *L. camara* is associated with human induced disturbance. Fruits are widely dispersed by many birds including introduced species. On the Galapagos *L. camara* started to spread soon after its introduction. In scrub areas of New Caledonia the plant scrambles through the vegetation not unlike climbers. However in taller forests it is absent and is rarely found in large treefall gaps. In areas where natural fires occur they stimulate thicker regrowth.

Site and climate

Tolerates a wide range of climates. In Australia *L. camara* tolerates a mean annual rainfall from 4000 mm to less than 1000 mm. Found between sea level and nearly 1000 m on Hawaii and higher in East Africa. Its distribution is affected by soil type, but grows well on poor soils.

Floristic region and vegetation types
A wide array of regions and vegetation types at the exception of closed forests and wet communities.

Pests and diseases
No reports of important pests and diseases.

Impact on ecosystem
The spread of *L. camara* on the Galapagos islands is seen as a threat to bird breeding populations and plant communities containing rare endemics. Its extensive seed production favours rat populations. In New Caledonia, by increasing fire intensity as a result of its large dry biomass as well as its smothering effect, it displaces natural scrub communities.

Impact on humans and related activities
L. camara poisoning in cattle and sheep have often been recorded. Children have died after eating unripe berries. The dense thickets, particularly those of the thorny variety, deter human access. In forestry it tends to over-run young plantations and prevents access to older plantations. In Indian sandalwood forests the shrub competes with the tree crop as well as favours the spread of the sandal spike disease. In some mountainous areas (Tanzania, India) the presence of *L. camara* was once considered as a good erosion preventing ground cover. It encroaches agricultural land, reduces the carrying capacity of pastures and is a weed in many agricultural crops. In New Caledonia following reproduction the climbing stems dry out and the dead material falls to the ground increasing fire susceptibility. In Tanzania *L. camara* can be considered as a serious health threat, as its thickets provide breeding grounds for Tsetse flies infected with trypanosomes of domestic animals.

Control
Since the turn of the century, biological control has been attempted in many parts of the tropics with varying degrees of success as different cultivars display differences in susceptibility to insect herbivores. Greater success appears to have been achieved in drier areas. In Uganda the introduction of *Teleonemia scrupulosa* Stal, used harmlessly in Australia and Fiji, was less successful as it attacked the crop *Sesamum indicum* L. Chemical control is expensive and cleared areas are rapidly reinfected by seedlings and stem and roots freely coppice. Mechanical control can be effective , particularly where land is cleared, but is labour intensive and requires continual follow-up treatment to remove roots and seedlings.

Ecological differences

Existence of ecological equivalent species and competitive interactions in invaded regions
Differs from native plants by a combination of fast growth rates, allelopathy, fire tolerance, and great variability (i.e. numerous cultivars).

Differences in status and ecology between invaded and native ranges
There are no indications that any major differences exist between the invaded and native ranges.

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Pierre Binggeli

October 1999

Leucaena leucocephala (Lam.) De Wit (Mimosaceae)

L. glauca (Willd.) Benth.

A widely planted multipurpose tree from tropical America introduced to most of the tropics. Forms monotypic stands in dry lowland areas of oceanic islands and regenerate freely in most of the tropics.

Species characteristics

Life form, size, lifespan
Deciduous tree usually growing to 9 m and in places up to 18 m high.

Taxonomy, variation and plasticity
Two subspecies of *L. leucocephala*, *leucocephala* and *glabrata*, are recognized. The former is shrubby. The species is evergreen when moisture is not limiting.

Reproductive biology
Globular flower heads contain numerous tiny hermaphrodite white flowers. Largely self-fertilised and self-compatible but hybridization with other species of the genus occurs readily. The 18 cm long pods contain about 20 seeds (size: ca 7 x 3 mm) and are borne in clusters of around 20. Germination rates vary from 5% to 90%. Flowering starts within a year of germination and after two years trees produce fruits all year round. Flowering increases under moisture stress or with the onset of shorter days in the sub-tropics. In India there are two flowering and fruiting seasons with a period of around four months separating flowering from pod dehiscence.

Resilience and resistance
Leaves are shed as a result of light frosts and after a heavy frost all above ground growth will die but the crown will survive and sprout vigorously the following year. Some Mexican provenances appear to be more frost tolerant. Stem and crown cuttings root and tree coppices well when cut and after fire. This very deep-rooted species fixes nitrogen and is drought tolerant even at the young seedling stage.

Environmental requirements and successional status
L. leucocephala has moderate tolerance for shade as it can regenerate under its own canopy and under *Lantana camara*.

Products and uses
It is used as a shade plant in coffee, rubber, cacao and cinchona plantations, for reforestation, windbreaks and firebreaks. Necklaces are made with the seeds.

Status in native range

Range and abundance
The extent of its range is uncertain but it is native to Mexico and probably to Central America and West Indies. The origin of this tetraploid species is unknown.

Climate
The climate is seasonal with a 3-6 month dry season and a rainfall of 750-1800 mm. The altitudinal range is the main difference between subspecies *leucocephala* and *glabrata*. They grow from sea level to, respectively, 500 and 1500 m.

Site requirements
It forms thickets in dry limestone and dry coastal regions of Puerto Rico.

Weediness
In Puerto Rico commonly found along roadsides and abandoned pasture.

Pests and diseases
Several pests and diseases affect *L. leucocephala* including a leaf spot disease *Camptomeris leucaenae*.

Status in invaded regions

History of introductions and intensity of invasions
Extensively planted worldwide and presently covering up to 5 million ha. Until the end of the 19th century all introductions were of the shrubby type but subpecies *glabrata* has been widely introduced over the past three decades. Introduced to the Pacific islands by the Spanish who over 400 years ago transported *L. leucocephala* feed and seeds to the Philippines. Introduced to Hawaii in 1864 and to the Marquesas Islands prior to 1893. It is now common in the lowlands of many Pacific islands often forming monotypic stands. In India it is thought to be a weed with tremendous natural regeneration.

Patterns of invasion and time-lag
L. leucocephala invades cleared areas and forms dense thickets. In the Hawaiian islands it sometimes becomes the dominant part of the vegetation at low altitude (0 - 300 m) on dry and disturbed sites. In the Marquesas Islands the tree is spreading into native disturbed forest. Plant growth is very variable. In poor conditions it is vulnerable to weed competition and wildlife. In India the tree spread into fallows within a few years of planting although no regeneration was recorded beyond a distance of 40 m. The species was reported to be abundant soon after its introduction to Hawai'i. During the 1980s crown dieback observed in many parts of Hawai'i it appears that trees with an understorey of shallow

rooted naturalised succulents suffered from less dieback and were more vigorous than with a grassy understorey. The differing water requirements between the succulents and the grasses may explain these observations.

Site and climate
In Hawai'i it is naturalised at sites which receive only 300 mm rain per year. Under cultivation it performs well in regions with a mean annual rainfall ranging from 650 to 3000 mm. Grows on a wide variety of soils.

Floristic region and vegetation types
Lowland vegetation on many Pacific Islands is now almost entirely dominated by introduced species. On the Marquesas Islands the dry lowland forests contain 28 woody species of which 9 are aliens. The lowland vegetation of Hawai'i has been much altered and is now dominated by exotics.

Pests and diseases
In Hawai'i an introduced beetle larvae destroys seeds and nearly all pods are infested. Since 1983, the psyllid *Heteropsylla cubana* from Cuba has been rapidly spreading westward throughout the Pacific and tropical Asia. Particularly in dry regions it results in total defoliation, death of terminal shoots and inhibits flowering, and repeated attacks result in tree death.

Impact on ecosystem
Although the impact of *L. leucocephala* on the invaded ecosystem has not been reported in much detail, it is clear that the tree, as well as other introduced species, displaces the native lowland vegetation of Pacific islands. Under a L. leucocephala canopy, which is relatively open, the soil is often free of vegetation.

Impact on humans and related activities
Once considered as the 'miracle tree' because of the variety of uses, including, firewood, timber, human food, green manure, shade, erosion control and forage. However both the foliage, high in protein and vitamin A, and the edible seeds contain the toxic amino acid mimosine and therefore can be toxic in large quantities. Horses, feeding on the tree, lose their hairs. In the Marquesas Islands farmers consider the species as an agricultural weed which is nearly impossible to uproot completely.

Control
A clear conflict of interest between the agroforestry value of the tree and its deleterious environmental impact can be seen in the practitioners attitude towards the psyllid *Heteropsylla cubana*. Agroforestry has suffered from serious economic losses, in Java estimated at $ 2.8 million between 1986 and 1988 as a result of the pest and biological control programme of the insect have been initiated. On the other hand managers of some Pacific islands, where *L. leucocephala* is considered a weed, would consider the arrival of the psyllid as beneficial. In western Africa the tree grows freely both from seed and cuttings, the plant becomes a pest difficult to eradicate from cultivated land.

Ecological differences

Existence of ecological equivalent species and competitive interactions in invaded regions
L. leucocephala and other woody invaders of lowland dry vegetation of oceanic islands probably have some, as yet undetermined, competitive advantage over native species and/or native species lack the characteristics necessary to cope with high levels of human disturbance.

Differences in status and ecology between invaded and native ranges
No differences have been reported.

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Pierre Binggeli

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Maesopsis eminii Engler (Rhamnaceae)

A large African tropical forest tree introduced to various parts of the tropics for timber production or as a shade tree. Naturally regenerating in many places and invasive in the rain forests of the East Usambaras (Tanzania).

Species characteristics

Life form, size and lifespan

Large canopy tree reaching a height of up to 43 m and a diameter of 1.2 m. Exceptionally able to live up to 200 years.

Taxonomy, variation and plasticity

The genus *Maesopsis* is monospecific. On the basis of height and wood quality variation a western African sub-species (*M. eminii* subsp. *berchemoides* Hallé) has sometimes been recognized. Tree height increases from about 15 m in western Africa to over 40 m in East Africa. The size and the dentation of the entire leaf exhibit much variation. The species is either deciduous or semi-deciduous depending on local climatic conditions.

Reproductive biology

The sex expression and pollination system is poorly understood but flowers are thought to be hermaphrodite and protogynous and insects are the likely pollinating agent. Flowering and fruiting starts after four to ten years and large seed crops are produced every year often every six months. A number of birds, including hornbills, and monkeys dispersed the large drupe (2-3 cm). Seeds remain dormant for up to at least 200 days. Germination is not triggered by light but appears to be affected by lunar cycles and enhanced soil humidity promotes early germination.

Resilience and resistance

Coppices freely after being cut and is susceptible to fire.

Environmental requirements and successional status

Usually described as a pioneer M. eminii germinate and seedlings survive under forest canopy for a few months. However, to grow and reach canopy height *M. eminii* requires large canopy gaps. At the forest-savanna boundary it becomes established under shrubby vegetation.

Products and uses

Timber is soft but firm and strong, and widely used in Uganda. However, the wood is not resistant to termites and fungal decay. *M. eminii* has been used in eastern Tanzania and Fiji in forestry plantation. It is used in India as a shade tree in coffee plantations and elsewhere in Asia as an agroforestry tree.

Status in native range

Range and abundance

M. eminii is widely distributed throughout moist tropical Africa from Liberia to Uganda and south to Angola. Usually an uncommon tree with the exception of the forest-savanna boundary in Uganda where it may be dominant.

Climate

Broad spectrum of climate requirements from per-humid tropics to seasonal tropics.

Site requirements

In moist forests *M. eminii* becomes established in large forest gaps. In Uganda, it does not regenerate in grassland mainly because of its susceptibility to fire. At these sites the grassland must be colonised by fire resistant species before *M. eminii* regenerates to form dominant stands. Subsequently succession proceeds to a high forest containing only a small proportion of *M. eminii*. On Lake Victoria islands succession from grassland to forest is similar except that it normally takes place around anthills. This suggests that higher nutrient status is necessary for tree colonisation to occur.

Weediness

In most of its native range *M. eminii* has no weedy tendencies, on the contrary it is usually scarce even in secondary forests.

Pests and diseases

Many insects and fungal diseases affect *M. eminii* causing defoliation, stem breakages and bark cankers.

Status in invaded regions

History of introductions and intensity of invasions

Introduced, probably from the Bukoba regions in western Tanzania, to the Amani Botanic Gardens in the East Usambara (eastern Tanzania) in 1913 when a 1 ha forestry trial plot was set up. Large-scale forestry planting was undertaken during the 1960s and early 1970s. *M. eminii* is now dominant in secondary forests near the *M. eminii* plantation and is found in many natural forest treefall gaps.

Natural regeneration and spread observed in Rwanda, Fiji, India and on Pemba Island (Tanzania). In Puerto Rico it regenerates profusely and is likely to become common or abundant in forests within the next century.

Patterns of invasion and time-lag
In the natural forest in the East Usambaras *M. eminii* becomes established in large treefall gaps and pit-sawing gaps where light levels are high. Seedling establishment occurs on bare humus soil. Less than 15 years lapsed between the introduction of *M. emini*i until it was first reported as regenerating in the natural forest.

Site and climate
Mountainous area at an altitude of ca. 1000 m. The climate is seasonal and frost-free with two rainy seasons and the annual rainfall varies between 1,000 mm and 2,000 mm.

Floristic region and vegetation types
The East Usambaras are part of the isolated Eastern Arc Mountains of Eastern Africa. Their sub-montane forests contain a number of endemic or near endemic species and have a high conservation value.

Pests and diseases
Little damage occur apart from limited fungal attack on young seedlings and some squirrel seed predation.

Impact on ecosystem
M. eminii becomes dominant in logged forests and regenerates in treefall gaps. It alters soil properties and associated fauna. Impact on tree regeneration probable but evidence inconclusive.

Impact on humans and related activities
In the East Usambaras people have no use for the wood, including as firewood, and do not exploit it. Farmers or foresters do not consider *M. eminii* as a pest as the tree does not have thorns or any other obvious negative effects on human activities.

Control
As yet no control programme has been initiated. Since the tree coppices readily, felling stands dominated by *M. eminii* must be accompanied with bark removal of stumps. Ring barking does not lead to crown death unless the cambium and part of the xylem are cut. Trees may be killed using arboricide.

Ecological differences

Existence of ecological equivalent species and competitive interactions in invaded regions
In the East Usambaras no equivalent species exist. A combination of very fast growth rates (in full light), large bird-dispersed fruits and seeds, short-term (few months) shade-tolerance in newly germinated seedlings and shade intolerance thereafter are a unique combination of characteristics in *M. eminii*.

Differences in status and ecology between invaded and native ranges
In the East Usambaras *M. eminii* does not appear to suffer from any significant attacks from pests and diseases similar to those reported from Uganda. Regeneration in treefall gaps, common in the East Usambaras, is scarce in the native range. *M. eminii* dominance in secondary vegetation is never observed in native range.

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Pierre Binggeli

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Melaleuca quinquenervia (Cav.) S.T. Blake (Myrtaceae)

Australasian tree forming large monospecific stands in swampy areas of southern Florida. The tree is compressing the distribution of a poorly-adapted swamp tree to wetter areas.

Species characteristics

Life form, size, lifespan

Evergreen tree to 20-25 m tall.

Taxonomy, variation and plasticity

M. quinquenervia is one of a group of several closely related species. It has frequently been confused with *M. viridiflora* and intermediates between the two have been reported.

Reproductive biology

The tree reaches sexual maturity within two years. Spikes bear white malodorous flowers with large stamens. The flowers produce large quantities of pollen and nectar and are pollinated by bees. The fruit is a woody capsule (4 mm) containing many minute seeds (<1.5 mm, 30,000 seeds g-1). Seeds have no special buoyancy structures and are usually poorly dispersed but in hurricane winds seeds can spread up to 7 km. Seeds may be retained in the seed capsule for several years, with up to 20 million seeds stored per tree. They are generally released when flow of moisture from the tree to the capsule is interrupted by the death of the branch usually as a result of fire or frost. However, some continuous seedfall has been observed with seasonal peaks. In Florida 10-20% of released seeds germinate. Seedlings grow up to 2 m per year.

Resilience and resistance

Resistant to wind, drought, fires and salt water. It has only slight resistance to frost although rootstock survives and sprouts. Coppices from cut stumps. The thick spongy bark of the trunk is fire proof but the outer layer highly flammable. The leaves and branches are killed during fires but are rapidly replaced by sprouts. Under flooded conditions fibrous roots are formed at the base of the trunk.

Environmental requirements and successional status

Species becomes locally dominant in swampy areas over a wide geographical area. It successfully competes with and outgrows other vegetation.

Products and uses

The wood is used for a number of purposes in Australia. It is suitable for windbreaks and beach planting. The papery bark is used as fruit packing material and torches.

Status in native range

Range and abundance

Native to eastern Australia, Papua New Guinea and Irian Jaya and often forms pure stands. It is relatively common throughout its range. Formerly thought to occur in New Caledonia, where the tree is now considered to be a distinct species.

Climate

Grows at an altitude of 5 - 100 m. It has broad mean annual temperature (18°C to 34°C) and rainfall (1000 mm to 5000 mm) requirements. Climate is monsoonal in the tropical part of its distribution.

Site requirements

In Australia the tree is sometimes considered to be fire intolerant and natural stands, which are often pure, are confined to wetlands. It occurs most frequently on peaty humic gleys, sandy at the surface but with silt or clay below and with a high organic component.

Weediness

Not reported in Australia.

Pests and diseases

In Australia insects significantly reduce girth, height and biomass increment in saplings.

Status in invaded regions

History of introductions and intensity of invasions

Introduced to Florida as an ornamental in 1906 in at least two coastal locations. Seeding from airplanes was carried out in the 1930s and in the 1940s trees were planted inland. In Hawai'i over 1.7 million trees have been planted in forestry plots and species is now naturalized in undisturbed mesic forest (altitude 30-890 m). First cultivated in 1920 using seeds from Florida.

Patterns of invasion and time-lag

The seasonal water regime and frequency of fire are the major factors determining the suitability of sites for *M. quinquenervia* establishment. The rate of spread of the tree increased dramatically with increased fire regime and the creation of new invasion foci resulting from natural seed dispersal. For many years *M. quinquenervia* caused no problems in Florida.

Site and climate

Southern Florida consists of a large swampy lowland region where slight changes in elevation alter the water regime which affects drainage, fire and salinity. The climate is sub-tropical with an annual rainfall of 1600 mm falling mostly between May and October. Occasional frosts occur.

Floristic region and vegetation types
The slight difference in elevation and associated variation in water regime result in a number of vegetation types including mangroves, marshes and forests. The Florida vegetation is isolated from other sub-tropical regions of northern America and is rich in endemics but prone to invasions.

Pests and diseases
Free from insect herbivory.

Impact on ecosystem
M. quinquenervia displaces native vegetation particularly *Taxodium distichum* var. *nutans*, a temperate tree at the limit of its range. Its dense canopy casts deep shade, and in association with its likely allelopathic properties, restricts ground vegetation. It is poorly utilized by wildlife. By increasing the forest cover it could result in higher demand for ground water and lowering of the water-table.

Impact on humans and related activities
Was considered to be a worthwhile and beneficial plant prior to its spread. Presently has no commercial uses but could be used for cellulose or as a fuel. As a nectar and pollen source it is important to the beekeeping industry. It appears to be a respiratory irritant when found close to human habitations and seems to repel mosquitos.

Control
In Florida current management programmes include a mixture of manual, mechanical and herbicidal control. Biological control is under study and a number of insect species are being evaluated in Australia. Since fire frequency is determined by water regime and water regime can be altered in large areas of southern Florida, water management is a possible means of limiting the spread.

Ecological differences

Existence of ecological equivalent species and competitive interactions in invaded regions
M. quinquenervia becomes dominant on the ecotone between dry pine forests and swamp forest where the conditions are either too wet for pine or too dry for *Taxodium distichum* var. *nutans*. There appear to be few fire-tolerant tree species particularly suited to the south Florida environment, including *T. distichum* which phenology is out of phase with the local environment.

Differences in status and ecology between invaded and native ranges
It has been suggested that in Florida trees are quite different in appearance from those observed in Australia. They are generally taller, straighter and form very dense populations and grow much faster. This appears to result from the absence of herbivory. Differences in fire tolerance between Florida and Australia may also be attributable to differences in herbivory. Climatic conditions in Florida and in New South Wales, where the seed source originated, are similar.

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Pierre Binggeli

May 1997

Miconia calvescens DC. (Melastomataceae)

M. magnifica Triana

Small tree from the neotropics invading disturbed areas and natural forests in the Society and Hawaiian Islands. It regenerates freely under canopy to eventually form monotypic stands. Many endemic species are being displaced and are thought to be at risk.

Species characteristics

Life form, size and lifespan
Small tree, up to 15 m tall, bearing large leaves (up to 1 m long) which are often green with three pale green nerves above and purple-blue below.

Taxonomy, variation and plasticity
Trees with bicoloured leaves are restricted to Central America while the other form occurs in both Central and South America.

Breeding system and reproductive biology
Small white and slightly fragrant flowers are borne in large panicles. Both allo- and autogamy occur, particularly in isolated individuals. Infructescences bear up to 500 blue-black fleshy berries (ca 0.6-0.7 cm in diameter) each containing around 140-230 seeds (size 0.7x0.5 mm). Flowering and fruiting may start within four years of germination. In Tahiti there are at least three peaks of flowering and fruiting per year. During the first fruiting season a young tree produces around 200,000 seeds on two infructescences and when older over 5 million seeds per year. Seed dispersal agents include gravity, wind, water, birds (mainly introduced species in the Society Islands) and small mammals, the latter two being the main agents. In Tahiti *M. calvescens* produces a large seed bank (up to 50,000 seeds m-2) where seeds are viable for more than two years and seeds germinate from fruits left in water for three months. Germination (rate up to 90%) is staggered and may take place under all light regimes including low light intensities (down to 0.02% of full sun light). Microsite requirements are varied and germination may even take place on rocks and the bark of trees.

Vegetative propagation
Vegetative layering and resprouting occur.

Light requirements and successional status
Miconia is shade-tolerant but it regenerates freely and grows more rapidly in forest gaps and open areas. In its native range is commonly found in disturbed areas.

Pests and diseases
No information is available.

Mycorrhizal associations and nitrogen fixation
Not reported.

Products and uses
Introduced to European botanical gardens and commonly cultivated in greenhouses because it had "one of the best and most striking of all conservatory foliage objects". Currently sold as an ornamental plant in the tropics.

Status in native range

Range and abundance
Natural distribution extends from southern Mexico (18o N) to southern Brazil (26o S). It is absent from most of the Amazon basin and the north coast of South America.

Climatic requirements
Its distribution suggests a wide climatic amplitude with a preference for tropical climates with distinct seasonality.

Site requirements
Generally found in old pastures, forest edges, river banks, trailsides, roadsides and disturbed areas and sometimes in natural forest from sea level to 1800 m.

Weediness
This species is never common even in disturbed areas.

Status in invaded regions

History of introductions and intensity of invasions
Introduced to Tahiti in a private botanic garden in 1937 and some years later planted at the Agriculture Research Station (Taravao). Introductions to the nearby islands of Moorea and Raiatea are thought to be the result of, respectively, wind-dispersal or hikers and contaminated soils (coffee and timber saplings).

Patterns of invasion and time-lag
In Tahiti, the spread of *M. calvescens* was not noticed until 44 years after its introduction, however by that stage the species was already widespread. In Hawaii *M. calvescens* began to spread as soon as the introduced trees started fruiting and this would suggest that in the Society Islands the observed time-lag is not an ecological phenomena but, rather, a human perception problem. In Hawaii the plant was detected twenty years after its introduction and only following warnings emanating from French Polynesia as to the threat posed by the species.

In the Society Islands *M. calvescens* has spread into disturbed areas (i.e. roadsides, abandoned pasture and forest edges) and into natural forests. In forests it regenerates under canopy, and became the dominant canopy tree over large areas of Tahiti particularly after hurricane-induced disturbance. The ability of *M. calvescens* to dominate oceanic island tropical rain forests is linked to the low stature of the trees found in these forests.

Range and abundance
It dominates forests over 70% (ca 70,000 ha) of the island of Tahiti.

Site and climate
The climate of the Society Islands is tropical oceanic with two seasons, one warm and humid and the other, between March and November, is cooler and drier. Mean annual temperature is 26°C and rainfall varies greatly with an average of 1700 mm/yr. *M. calvescens* is found between 10 and 1300 m a.s.l. and in areas with more than 2000 mm of rainfall per year.

Floristic region and vegetation types
The Society Islands have 623 native species, of which 273 are endemics, and over 1500 species have been introduced. The original vegetation was dominated by forests.

Pests and diseases
Specific natural enemies have not been found.

Impact on ecosystem
M. calvescens has dramatically altered natural forests of the Society Islands. Native species are unable to tolerate the heavy shade cast by *M. calvescens* and are displaced. As a result, half of all endemic species are though to be at risk. The superficial and tentacular rooting system is thought to contribute to landslides.

Impact on humans and related activities
No obvious negative effects besides altering the physiognomy of the forested landscape.

Control
In the Society Islands and Hawaii major educational and control programmes have been initiated. Besides preventing the introduction of *M. calvescens* to other islands, eradication of the species from lightly infested islands has been attempted. Small individuals are uprooted while large one are cut and treated with herbicide (2,4-D) to prevent resprouting.

Ecological differences

Existence of ecological equivalent species and competitive interactions in invaded regions
No native species appear to have life history characteristics (rapid growth (up to 1 m/yr), small seeds, profuse seed production, seed bank, shade tolerance etc.) similar to those of *M. calvescens*.

Differences in status and ecology between invaded and native ranges
In the neotropics *M. calvescens* is not abundant and never dominates vegetation as it does in Pacific islands and this may result from the absence of natural enemies in the introduced range. The altitudinal range of the species is wide in both the native and introduced ranges.

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Pierre Binggeli

May 1998

Mimosa pigra L. (Mimosaceae)

Thorny shrub from tropical America rapidly spreading in northern Australia and Thailand. In Australian floodplains it forms self-regenerating monotypic stands.

Species characteristics

Life form, size, lifespan

Spreading thorny shrub usually up to 2 m tall but occasionally to 6 m. Maximum age is about 5 years.

Taxonomy, variation and plasticity

There are two varieties, var. *pigra* and var. *berlandieri* which differ slightly in pod pubescence and spine morphology. Only the former has spread around the world.

Reproductive biology

Flowering may start within a year of germination. The bee-pollinated inflorescences, containing up to 100 flowers, are spherical, pink and last one day. On main branches one inflorescence is produced daily for five months during the rainy season. In Australia it has been suggested that most of the seeds are produced by autogamy, although wind pollination can not be ruled out. The hairy pods are up to 15 cm long and contain 8 to 24 seeds (each seed is ca. 5 x 2.4 mm and weighs 0.09 mg). The fruits ripen in ca. 3 months and when mature fragment into indehiscent one-seed segments. The bristles covering the pods facilitate floating and enhance dispersal along river systems. In evergreen forests a few flowers and fruits are found throughout the year. In Australasia in permanently moist sites flowering occurs all year round and on average < 5% of flower buds produce seeds. Anthesis takes place about 8 days after bud formation and another month is necessary for the production of mature seed pods. In northern Australia the soil seed banks can reach up to 12 000 seeds m-1 and seeds remain viable for more than two years. Seeds generally germinate when they are first wetted and the germination rate is high.

Resilience and resistance

In seasonally flooded areas fibrous adventitious roots develop around the base of the multiple stems. Mycorrhizae have been found associated with few strains of *Rhizobium*. However these associations are rare and it is not clear how important a source of nitrogen they are to populations of *M. pigra*. Following natural fires the plants resprout freely. The shrub does not naturally reproduce vegetatively.

Environmental requirements and successional status

Although adapted to seasonally flooded habitats M. pigra can regenerate under some degree of canopy cover.

Products and uses

It has been used as green manure and cover crop and is used as firewood and bean poles in Thailand. Utilized against snake bites.

Status in native range

Range and abundance

Native to Mexico, Central and South America

Climate

Dry to seasonally wet.

Site requirements

In Costa Rica the *M. pigra* natural habitats are the banks of large rivers and marsh edges. Currently occupying similar habitats such as road sides and marshy spots in open pastures.

Weediness

In Costa Rica *M. pigra* is probably much more common now than prior to European colonisation. Its seeds appear to be spread by road construction equipment and thus the plant is typical of roadsides.

Pests and diseases

Leaflets fed upon by a number of beetle species but avoided by cattle and horses. In Costa Rica, seeds are heavily predated by beetles.

Status in invaded regions

History of introductions and intensity of invasions

M. pigra is widely distributed in Africa but unclear how it got there from Tropical America. Introduced, as an ornamental or seed contaminant, to the Darwin Botanic Gardens of Australia's Northern Territory prior to 1891. The spreading population is thought to be the result of a single introduction. During the second part of this century *M. pigra* has spread dramatically to form monotypic stands in floodplains. Introduced to Thailand in 1947 as green manure and cover crop and being prickly it was thought it would restrict access to water banks as thus reduce erosion. Now it covers large areas of standing waters and water banks. Also spreading in Indonesia and peninsular Malaysia. Long-distance dispersal is possible when cattle are transported and in Thailand road transportation spread seeds along highways.

Patterns of invasion and time-lag

Although introduced to Australia last century *M. pigra* remained an occasional nuisance around Darwin. It started to spread in the late 1950 when it reached the open floodplains and started to spread to increase dramatically in the 1970s. The time-lag resulted from the inability of the species to reach suitable habitats. The rate of population increase is high (r of ca. 0.66 per year). Once established as monotypic stands, *M. pigra* can regenerate under its own canopy. In these stands the half life of plants taller than 20 cm varies between 13 and 22 months depending on soil types. *M. pigra* can also regenerate under canopy of *Melaleuca* fringing the floodplains.

Site and climate
M. pigra is found in tropical regions with > 750 mm annual rainfall unless growing around dams and watercourses. It does not appear to have any soil type preferences, but is more commonly found in moist situations such as floodplains and river banks.

Floristic region and vegetation types
It invades sedgeland and grassland communities on open floodplains and *Melaleuca* forest fringing the floodplains. It is not found in tropical rain forest areas (rainfall > 2250 mm).

Pests and diseases
Ungulates have little impact on *M. pigra* and some post dispersal seed predation occurs.

Impact on ecosystem
M. pigra completely alters floodplain and swamp forest of northern Australia. Its main impacts are: fewer birds and lizards, less herbaceous vegetation and hinders tree regeneration. If the spread *of M. pigr*a is not halted it may affect the touristic value of the Kakadu National Park as many visitors come to see the wetlands birdlife. In Thailand it interferes with irrigation systems (sediment accumulation) and access to electric power lines and is a safety hazard along roads. It also grows in fallow rice paddies making reclamation more expensive. It is a source of firewood and bean poles and its foliage can be used as an animal feed.

Impact on humans and related activities
In Australia M. pigra poses a threat to the cattle industry as it invades buffalo pasture. It also restricts access to waterways for humans, particularly fishermen.

Control
In Australia Neotropical biological control agents are being actively investigated as classical introductions while chemical control is used to contain the spread and eradicate new infestations. Aerial spraying of gelled gasoline followed by fire kills stands of *M. pigr*a and soil surface seeds, however it enhances buried seed germination. Effective control is difficult because of the large soil seed bank.

Ecological differences

Existence of ecological equivalent species and competitive interactions in invaded regions
In the floodplains of northern Australia there are no woody plants present.

Differences in status and ecology between invaded and native ranges
The main difference appears to be habitat availability. In northern Australia large treeless floodplains exist which doe not appear to be the case in tropical America. A comparison of phytophagous insect fauna between Australia and Mexico showed that in the invaded region there were fewer insect species, more species were polyphagous and fewer feed externally. In Mexico many insects feed on new growth and inside the reproductive structures but such damage was not observed in Australia.

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Pierre Binggeli

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Myrica faya L. (Myricaceae)

Macaronesian endemic introduced to Hawai'i in the 19th century. Following extensive reclamation planting, it has spread into a variety of habitats including natural forest, lava flows, roadsides and abandoned pasture.

Species characteristics

Life form, size, lifespan

Evergreen tree to 12 m tall. Often multi-stemmed.

Taxonomy, variation and plasticity

No information is available. However the species is found on isolated islands and under varying climatic conditions and this would suggests that some variation must exist between provenances.

Reproductive biology

M. faya is considered to be a dioecious species, however 'male' plants often produce some fruits and 'female' individuals a few male inflorescences. It appears to be a wind-pollinated species although in Hawai'i it is visited by the introduced *Apis mellifera*. The edible black drupe (6mm in diameter containing 1-5 seeds) is bird-dispersed in its native range but in Hawai'i it is dispersed by birds (mainly introduced) and feral pigs. About 20,000 seeds per tree are produced every year. In Hawai'i fruits ripen primarily between August and November but may be produced all year round. Seed germination decreases from 80% at 10 weeks to 30% after 78 weeks of dry storage. Passage through birds has no effect whereas its own leaf litter reduced germination. Germination occurs at all light levels but is highest under 55% and 63% of shade.

Resilience and resistance

Nitrogen fixing species which can colonize lava flows. In the Azores it is wind resistant although the bushes are only 2-3 m tall and are much flattened and bent. Allelopathic effect has been suggested. Burnt trees may resprout.

Environmental requirements and successional status

Although adapted to colonize old lava flows, *M. faya* is a main component of old forests. Regenerates freely under open canopy but not under full canopy.

Products and uses

In Hawaii Portuguese labourers made wine from the fruit.

Status in native range

Range and abundance

Restricted distribution to the Macaronesian islands of the Azores, Madeira and the Canary Islands. The tree is common in most remaining evergreen forests.

Climate

In Canaries the climate is typically mediterranean with wet winters and dry summers. The climate of the Azores is affected by the Gulf Stream with no frost below 500 m and average summer and winter temperatures of respectively 21°C and 14.5°C. Madeira's climate is intermediate. Rainfall on all islands increases with altitude (varying between ca. 750 mm and 2500 mm) and highlands are often covered with cloud and mist.

Site requirements

In the lowland Azores, much altered by man, *Myrica faya* is the main species to have regenerated on old lava flows. Around an altitude of 600 m, where some natural forest remains, *M. faya* is codominant in the canopy (5-6 m tall) and sometimes is an emergent. Distribution up to 900 m a.s.l. The species does not appear to regenerate under canopy.

Weediness

No sign of weediness. In fact in the Azores the forests, where *M. faya* is codominant, are invaded by *Pittosporum undulatum*, native of eastern Australia.

Pests and diseases

Suffers from a number of diseases resulting in canker, dieback and root rot.

Status in invaded regions

History of introductions and intensity of invasions

Introduced into Hawaii by immigrants from the Azores and Madeira in the late 1800s, probably as an ornamental or medicinal plant. Extensively planted for watershed reclamation in the 1920s and 1930s. Now present on several Hawaiian islands and by 1985 covered 12,200 ha of the Hawaii Volcanoes National Park (HVNP) and considered one of the main noxious species. Common on pasture land.

Patterns of invasion and time-lag

On young, volcanically disturbed soils *M. faya* rapidly forms dense monotypic stands but does not readily invade closed, late-successional native forest. In HVNP birds disperse the seeds to perch trees, the native *Metrosideros polymorpha*. Under tree canopy seed densities of 6 to 60 seeds.m-2.yr-1 are found whereas they are absent in the open. Seeds germinate and seedling become established under *M. polymorpha* canopies.

Natural spread was reported within years of the watershed planting which was then halted. It was first reported in undisturbed areas of the HVNP in 1961 and by 1973 the population was large enough to warrant control.

Site and climate

M. faya is found between 150 to 1310 m a.s.l. in mesic to wet forest. At the altitude of 1250 m, where most of the HVNP invasion is taking place, the mean annual rainfall is ca. 2400 mm without a distinct dry season and the mean January and July temperatures are, respectively, 14°C and 17°C. Very occasional frosts occur.

Floristic region and vegetation types

The Hawaiian islands are rich in endemic species and are very susceptible to plant invasions particularly in lowland regions. Other woody plants are invading are invading plant communities invaded by *M. faya*.

Pests and diseases

Some seeds are eaten by rats.

Impact on ecosystem

M. faya changes ecosystem function by altering the nitrogen cycle. Its litter inhibits germination and seedling establishment of the native tree *Metrosideros polymorpha*. Monospecific stands have virtually no understorey.

Impact on humans and related activities

Not reported.

Control

In the HVNP control was initiated 22 years after *M. faya* was first recorded. Over four years 92,000 individuals were removed, yet 609 ha of moderate density populations remained and the control programme was abandoned. The use of chemical control in native vegetation, some of which is threatened or endangered, is avoided. Biological control of *M. faya* is being investigated.

Ecological differences

Existence of ecological equivalent species and competitive interactions in invaded regions

Apparently the actinorrhizal symbiosis, characteristic of M. faya and other species colonizers of low-nitrogen sites, was absent from the native flora of Hawai'i. In competition with the native tree *Metrosideros polymorpha*, *M. faya* diameter and height growth is always greater in all size classes.

Differences in status and ecology between invaded and native ranges

M. faya is invasive in Hawaii and is considered a weed whereas in the Azores, where it is native and codominant in evergreen forest, it often fails to regenerate and its habitat is invaded by *Pittosporum undulatum*. Both the native and invaded ranges are rich in endemic species but have relatively few tree species. The time-lag between the lava flow formation and *M. faya* colonisation appear to be much shorter on Hawai'i than on the Azores.

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Pierre Binggeli

May 1997

Passiflora mollissima HBK. Bailey (Passifloraceae)

Andean woody climber cultivated in tropical and warm-temperate zones for its edible fruit and attractive flowers. It has become a serious pest in the forests of Hawai'i.

Species characteristics

Life form, size and lifespan

Perennial woody vine reaching a length of 20 m and an age of 20 years. Usually climbing but in absence of support is either shrubby or trailing.

Taxonomy, variation and plasticity

In its native range *P. mollissima* is morphologically variable and frequently hybridizes with other species. In Hawai'i, at the exception of flowering and fruiting, the plant's phenology is variable. In East Africa two distinct forms occur.

Reproductive biology

The nectariferous flowers are large (5-10cm in diameter), pinkish, and borne singly at base of tendrils. They visited by a large number of insects and birds but are chiefly pollinated by honeybees and syrphids. Although mainly outcrossed, selfing occurs. Flowering and fruiting starts when the plant is one year old. The large yellowish fleshy fruits (5 cm) containing 180 seeds (? 6 mm) ripen in ca. 3 months and in Hawai'i are produced throughout the year with a peak during the wet season (December-March). Fruits are widely dispersed locally by native and alien birds and mammals but long distance dispersal also occurs. In New Zealand 50% of seeds survived burial for 66 weeks at 9 cm, and subsequently germinated. Seed germination is staggered with a peak within eight weeks following the breaking of dormancy.

Resilience and resistance

Has a high capacity for vegetative propagation, with the interconnected portions decaying. The plant is frost tolerant.

Environmental requirements and successional status

P. mollissima tolerates both high and low light levels. A seedling bank is commonly found under tree canopy although newly germinated seedlings do not tolerate dense shade. Optimal growth occurs in full sun light.

Products and uses

Species is widely cultivated in its native range and in many parts of the tropics and sub-tropics as an ornamental and for its fruits.

Status in native range

Range and abundance

Native to the tropical region of the Andes between 2000 and 3600 m a.s.l. Original distribution is unclear as the species has been widely cultivated. Natural populations are scattered and sparse.

Climate

Seasonal climate typically with a 2 months dry period and a mean annual temperature and rainfall of respectively ca. 13°C and ca. 1300 mm. *P. mollissima* tolerates occasional frosts.

Site requirements

Not known

Weediness

Not reported.

Pests and diseases

Fungal pathogens and insects attack the fruits.

Status in invaded regions

History of introductions and intensity of invasions

Introduced to many tropical countries. First introduced to the island of Hawai'i around 1920. Subsequently introduced to several other sites on Hawai'i and two other nearby islands. *P. mollissima* occupies large areas on three Hawai'ian islands and may form continuous cover. Described as weedy in some parts of New Zealand and appears to have naturalised in some South African forests. In East Africa it is cultivated as an ornamental and often escaped, growing in forest edges and clearings.

Patterns of invasion and time-lag

Establishment and growth of *P. mollissima* increase with increasing light intensity. The densest infestations are found in openings and forest margins. In the forest environment a seedling bank exist and the seedlings are released as soon as a gap is formed in the canopy. In smaller gaps *P. mollissima* may fail to reach canopy height prior to gap closure. Once the vines have reached canopy height, they spread laterally. Increased disturbance increases the rate of the invasion particularly as a result of feral pig activity, logging or hurricanes. It appears that no time-lag occurred in Hawai'i between the timing of the various introductions and that of the plant's spread.

Site and climate

In Hawai'i, *P. mollissima* occurs between an elevation of 500 and 2500 m. It tolerates a wide variation in climate with a range of mean annual rainfall and temperatures of respectively 1250-2000 mm and 11-24°C. Short dry season occurs in June-July.

In New Zealand the vine is found in areas with a mean annual temperature of 11.4 to 15.0°C and rainfall of 800 to 1200 mm.

Floristic region and vegetation types

The Hawai'ian islands are rich in endemic species but are prone to biological invasions by a wide array of plants and animals. *P. mollissima* is spreading into native forests, scrub vegetation, pastures, forestry plantations and lava flows.

Pests and diseases

Several fungal pathogens attack fruits but do not limit fruit production. In damper areas they suffer from slug herbivory.

Impact on ecosystem

In Hawai'i *P. mollissima* has a major impact on vegetation including suppression of tree regeneration, toppling of shallow-rooted trees, death of standing trees through shading and lowered species richness. Continuous prolific fruit production lead to an increase in population densities of exotic mammals, e.g. feral pigs.

Impact on humans and related activities

P. mollissima has no economic value in the tropics, while in New Zealand it is widely grown as a fruit and sold. It is a major problem in forestry, particularly following logging.

Control

Mechanical, chemical and biological means of control have been attempted with limited success in the tropics. In New Zealand cutting vines and wetting cuts with herbicide, particularly Tordon or Roundup, is effective although follow-up treatment may be required.

Ecological differences

Existence of ecological equivalent species and competitive interactions in invaded regions

There does not appear to be any ecological equivalent in Hawai'i.

Differences in status and ecology between invaded and native ranges

In Hawai'i, as opposed to South America, the species does not vary morphologically. Fruit set is greater in Hawai'i than in South America and this probably result from the lower insect herbivory suffered by flowers and fruits in the invaded range. Densities of *P. mollissima* in Hawai'i are far greater than those observed in the Andes.

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Pierre Binggeli

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Pinus patula Schiede & Deppe (Pinaceae)

Widely planted timber tree from the Mexican uplands. It is invading montane areas of Malawi and Hawaii. Its spread is facilitated by fire in grasslands and logging in natural forests. The tree's spread threatens some endemic.

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Species characteristics

Life form, size and lifespan

Evergreen tree 20 to 30 m tall.

Taxonomy, variation and plasticity

Sometimes difficult to distinguish from forms of related species. Some morphological characters show marked clinal variation in Mexico.

Reproductive biology

Flowering may start when the tree is two years old. Female flowers usually appear a year later than male flowers and are respectively borne in the upper and lower parts of the canopy. In Hawaii and Malawi *P. patula* starts producing many cones after 6 to 8 years. In Africa seed set varies from 45 to 93 seeds per cone out of a potential 200 to 300, whereas a Mexican collection had only 22 seeds per cone. Cones take 22 months to reach maturity and may remain closed several years until they are scorched by fire. Then the wind-dispersed seeds (4 mm long with a 1 cm long wing, weight = < 0.1 mg) are released and have a high germination capacity (ca 85%). In tropical Africa it appears to set seed freely every year in upland areas between 1000 to 1700 m.

Resilience and resistance

Although easily killed by fire, *P. patula* is adapted to it as its serotinous cones release seeds after burning and seedling establishment is favoured by bare mineral soil. It possesses mycorrhizal associations and plantations in Malawi failed until they were brought into the country.

Environmental requirements and successional status

The tree requires deep acidic soils with a good moisture supply. In Mexico it often forms monotypic stands or is found in mixtures with other pine species.

Products and uses

Important timber, pulpwood and fuelwood in many parts of the world.

Status in native range

Range and abundance

Native to the highlands of Mexico where it has a restricted distribution (18°N to 24°N). It forms pure dense stands.

Climate

Warm temperate region where the rainfall varies between 1000 and 2000 mm mainly falling during the summer months. Occasional frosts occur.

Site requirements

The species occurs mainly on the eastern side of mountains at an altitude between 1650 and 3000 m. It is found in areas with deep well drained sandy loam.

Weediness

Not reported.

Pests and diseases

Seed set often prevented by rust fungus.

Status in invaded regions

History of introductions and intensity of invasions

It is grown in many parts of the world in large plantations. First introduced to Malawi in 1923 and to Mount Mulanje (16°S, 35°E) in 1946 when forestry trial plots were established. In the 1950s large-scale forestry plantings were undertaken. Originally *P. patula* was planted as a nurse crop for the native timber tree *Widdringtonia cupressoides* (L.) Endl. but the objective was never achieved. In Hawai'i it invades native shrubland in the Haleakala National Park.

Patterns of invasion and time-lag

P. patula is spreading in both grassland and native forest. Regeneration is greatest in the vicinity of plantations but isolated trees became established several km away from the plantations and within 10 years became foci for further spread. In natural forest the pine density tends to increase with logging intensity. The current fire regime is the main factor facilitating the spread of this fire-adapted tree in grasslands. However, it appears that the increased dead matter increases the intensity of fires which has resulted in the death of some pine stands. The impact of variation in fire cycles and intensity on the invasion have yet to be investigated.

Site and climate

The Mulanje Mountain consist of a series of plateau around 1800 m with peaks reaching 3000 m. Mt Mulanje rises abruptly from the surrounding plain (600-700 m) and is isolated from other central African mountains. *P. patula* is found in a number of plant communities between 1800 and 2400 m. On most of the mountain rainfall is seasonal (mainly summer) and is around 2000-3000 mm per annum on the plateau where night frosts regularly occur. Soils (ferallitic latosols) are acidic (pH ca 4.2)

Floristic region and vegetation types
These mountains are covered by a variety of vegetation types varying with altitude, including forests and grasslands, containing a number of endemic species and invaded by several introduced species. The plateau vegetation is grassland, maintained by fire, and interspersed with forest in sheltered hollows and ravines. Lower elevation vegetation types, but particularly forests, are much destroyed and threatened by human activities.

Pests and diseases
The species is generally considered free of pests and diseases by foresters although lepidoptera do pose a threat in some regions.

Impact on ecosystem
There are indications that *P. patula* alters the species composition of invaded forest and grasslands and it appears to exclude some uncommon endemic ground flora species. It displaces *W. cupressoides*, Malawi's national tree, which although not endemic to Mulanje, only reaches its full height (ca 40 m) there. An important component of the shrub layer *under P. patula* is the invasive *Rubus ellipticus*.

Impact on humans and related activities
P. patula timber is worth twenty times less than that of *W. cupressoides*.

Control
Trees are cut near the ground and the slash is stacked in piles. Follow-up operations, preferably burning, are essential within a year or two to eliminate seedlings. The eradication of *P. patula* from Mt Mulanje has been recommended. Apart from control measures carried out by I. Sakai, a Japanese volunteer, and controlled yearly fires are lighted around the perimeter of the pine plantations killing young seedlings, the recommendations have not been implemented.

Ecological differences

Existence of ecological equivalent species and competitive interactions in invaded regions
There are no native pine species in Malawi. In the absence of *P. patula* and the native *W. cupressoides* would spread into the secondary scrub and occasionally into short grassland. Although highly susceptible to fire, *W. cupressoides* can become dominant if sufficiently fierce periodic fires occur to kill broadleaved trees. However, *W. cupressoides* is much slower growing than *P. patula* and in the presence of the latter succession will result in a *P. patula* dominated canopy. *W. cupressoides* competitive ability has been further diminished as it has recently suffered from the introduction of the cypress aphid, *Cinara cupressi*, resulting in the poor health or death of many trees.

Differences in status and ecology between invaded and native ranges
No apparent differences in site requirements or ecology between native and invaded regions exist. In its native range *P. patula* often compete with other pine species and seed set is affected by fungus.

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Pierre Binggeli

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Pittosporum undulatum Vent. (Pittosporaceae)

Large ornamental temperate/sub-tropical forest tree, native of south-east Australia. Introduced to various temperate and tropical regions including Jamaica, where it invades natural forest.

Species characteristics

Life form, size, lifespan

Large evergreen tree growing to 30 m, lifespan unknown.

Taxonomy, variation and plasticity

P. undulatum is well defined taxonomically, though it hybridises with *P. bicolor* and perhaps *P. revolutum* in Australia.

Reproductive biology

Sex expression of flowers is somewhat variable but flowers are usually unisexual. Inflorescences (cymose) bear between 1 and 4 insect-pollinated flowers. Flowering starts at around 5 years of age and is enhanced by higher light levels. Fruits (capsules, ca. 12 mm across) take about 6 months to mature. Fruiting is highly synchronised in Jamaica. The capsules usually contain 20-40 sticky orange seeds, which are bird-dispersed.

Resilience and resistance

Seedlings coppice if the shoot is removed and blown-down trees sprout vigorously along the trunk. Cut stems resprout if replanted. The species is moderately susceptible to fire. VA mycorrhizae have been observed on *P. undulatum* in Jamaica.

Environmental requirements and successional status

Seedling recruitment occurs below the forest canopy but increases in higher light intensities (i.e. in gaps) with seedling densities up to 5000 m^{-2}. Few seeds germinate under *P. undulatum* canopies. It can become dominant in Australia and elsewhere.

Products and uses

P. undulatum makes very good firewood, produces excellent charcoal and is a useful all purpose timber. It is an ornamental tree with attractive fragrant flowers. Abundant nectar production makes it good for honey bees.

Status in native range

Range and abundance

P. undulatum is native to the coastal belt and mountains of south-eastern Australia from Biggenden in Queensland to the south of Victoria. It is a common sub-canopy tree and shrub in several forest types and is also widespread in more open habitats.

Climate

The climatic conditions of its native range vary from moist sub-tropical to dry temperate (without a pronounced dry season).

Site requirements

P. undulatum is found in a variety of habitats, such as rain forest, scrub, gullies and grassland (if fire is suppressed). In the drier parts of the range it is restricted to moister sites. Fire limits its range and as the fire regime in the 20th century has decreased as a result of human management, *P. undulatum* has been able to spread to areas where previously it would have been killed.

Weediness

It is spreading outside its pre-European settlement range in several parts of Australia, a result of widespread planting in gardens, the fire suppression policies in many areas close to habitation and the introduction of the European blackbird, *Turdus merula*.

Pests and diseases

About 10 insect species in Australia feed on *P. undulatum* but none are believed to cause serious damage or death or significantly reduce population levels.

Status in invaded regions

History of introductions and intensity of invasions

Introduced to Jamaica in 1883 and planted in the Cinchona Botanic Gardens situated at 1450 m in the Blue Mountains. Found throughout a large part of the western end of the Blue Mountains and dominant in many areas of secondary forest close to Cinchona, locally common in more primary forest.

P. undulatum invades the Eucalyptus forests of central Victoria (Australia) where it is considered a threat to the survival of the native forests. It is invading a number of Pacific and Atlantic ocean islands. *P. undulatum* is spreading into scrub and riverine forest in Cape Province, South African fynbos but it has recently been affected by severe die-back.

Patterns of invasion and time-lag

P. undulatum seedlings emerge after periods of wet weather, but not beneath dense canopy cover. However the rate of spread of *P. undulatum* increases with large-scale disturbance such as that caused by hurricanes. Isolated *P. undulatum* trees occur several hundred metres from other trees of the same species.

There is no evidence for any appreciable time lag in the invasion, though the rate of invasion certainly appears to have accelerated since Hurricane Gilbert in 1988.

Site and climate

The Blue Mountains are very steep and rise to 2265 m. Mean annual rainfall is 2700 mm or more with two rainy seasons, though considerable variability in rainfall. Mean monthly maximum temperatures range from 18.5 to 20.5°C. Night-time temperatures in winter can fall below 10°C. Hurricanes are quite frequent.

Floristic region and vegetation types

The Blue Mountains are covered with montane rain forests containing about 550 flowering plant species, of which about 85 are thought to be endemic to the range. Canopy height ranges from 5 m or less at high altitude to 25 m plus lower down.

Pests and diseases

In South Africa die-back has occurred as a result of a recent spread of an unidentified disease.

Impact on ecosystem

P. undulatum becomes dominant in secondary forests and natural forest subjected to hurricane damage. In areas invaded by *P. undulatum* a sharp decrease in native species richness has been recorded, probably because of the dense shade it casts.

Impact on humans and related activities

P. undulatum wood is preferred by locals for firewood and may have potential as a source of timber.

Control

Control has not been attempted but would be desirable. However due to the steep slopes and inaccessibility of the Blue Mountains traditional methods of control would be difficult. Furthermore, gap formation following cutting promotes the regeneration of *P. undulatum* and other alien weeds, notably *Polygonum chinense* and *Hedychium gardnerianum*. Biological control is being considered.

Ecological differences

Existence of ecological equivalent species and competitive interactions in invaded regions

P. undulatum, when compared with native species, differs in its response to hurricane by lower mortality, less crown damage and higher rate of treefalls (trunks readily sprout after being blown down). Its crown is noticeably denser and extends further downwards than that of native species. The extensive superficial rooting system of *P. undulatum* is not observed in native species.

Differences in status and ecology between invaded and native ranges

The range in climates between its invaded and native ranges is considerable

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Pierre Binggeli & Tom Goodland

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Psidium guajava L. (Myrtaceae)

Small evergreen weedy tree from tropical America introduced throughout the tropics for its edible fruits. It is spreading in pasture and agricultural land. On the Galapagos it is displacing evergreen forest composed of many endemic taxa.

Species characteristics

Life form, size, lifespan

Evergreen shrub or small wide-spreading tree 3-10 m high.

Taxonomy, variation and plasticity

Numerous varieties including yellow and red fruited ones. All cultivars are vegetatively propagated.

Reproductive biology

The white flowers are ca. 1.5 cm in diameter and are found singly or in cymes of 2 or 3 flowers. Flowers are pollinated by bees and other insects and cross-pollination accounts for about 35% of the seed set. The large pear-shaped fruit (5 cm long) is an edible berry and contains numerous seeds (size 3-5 mm). It is mainly distributed by cattle. The seed passage through the animals digestive tract does not appear to affect seed germination but seed losses occur as a result of food mastication. Seeds remain viable for several months and will germinate in 3-5 weeks in the warm season. Seed germination rates vary much from year to year and seedling establishment in cow pats is reduced by as much as 50% as shoots of germinated seeds deeply buried in the dung fail to reach the surface.

Resilience and resistance

P. guajava often suckers from roots near the base of the trunk, particularly after a light frost, to which the tree is susceptible. It tolerates temporary waterlogging. Following cutting it coppices readily and the tree spreads by suckering. It can also be propagated by layering or cuttings. *P. guajava* possesses vesicular-arboricular mycorrhizal associations.

Environmental requirements and successional status

It has an excellent ability to compete with weeds and grass. It can take over sites when it receives full sunlight but can withstand partial shading.

Products and uses

The wood makes excellent firewood and charcoal, and tool handles and implements can be made out of it. The fruits have a very high vitamin C content and red guavas are rich in vitamin A. They are made into preserves, jam, jelly and juice. The tannin-rich leaves and green fruits are used for dyeing and tanning.

Status in native range

Range and abundance

Native to the American tropics where it is widely cultivated.

Climate

It grows well in tropical areas of more than 1000 mm of rainfall and can endure droughts of 4 to 5 months.

Site requirements

Found from sea level to 800 m and sometimes up to 1500 m, although its natural limit is unclear due to widespread planting. It favours slightly to strongly acid soils.

Weediness

It is a common pasture weed in central America either as scattered trees or in pure stands (264 trees/ha).

Pests and diseases

Many insects are reported to cause damage to the plant but particularly to its fruits.

Status in invaded regions

History of introductions and intensity of invasions

At an early date the Spanish brought *P. guajava* to the Philippines and the Portuguese to India, and it was then spread throughout the tropics. A tree from the Melbourne Botanic Gardens was introduced to Fiji in 1863, where the species has since become a major weed of pastoral, arable and plantation land. First introduced to the Galapagos around 1870 and is now found on three of the populated islands. It has invaded natural forest and covers large areas of these islands.

Patterns of invasion and time-lag

In agricultural areas it becomes a serious pest particularly as a result of root suckering induced by firewood cutting. It competes successfully with crop plants and grasses and soon forms thickets which smother grasses and reduce crop yields. In the Galapagos in 1922 it was already mentioned as a bad plague forming impenetrable thickets. It has replaced most evergreen forest on one of the islands and covers vast areas of the humid zones of four islands. The spread is facilitated by introduced cattle which eat the fruit and excrete the seeds. The dung provides a nutrient rich substrate and appear to reduce grass competition. Cattle also trample vegetation and create open spaces necessary for successful *P. guajava* seed germination and seedling establishment. Increased fire frequency increase *P. guajava* dominance.

Site and climate
In the tropics it becomes established under a wide variety of soil and climatic conditions, particularly rainfall.

Floristic region and vegetation types
Usually found on fallow land with highly modified flora. On the Galapagos the invaded vegetation contains a large number of endemic taxa and *P. guajava* is mostly found in the evergreen forest or scrub.

Pests and diseases
In Fiji *P. guajava* is attacked by the fungus *Botryodiplodia theobromae* which also attacks plantation crops. In India wilt is usually fatal where *P. guajava* occurs on soil with pH > 7.5.

Impact on ecosystem
On the Galapagos Islands *P. guajava* outgrows native species and forms dominant stands suppressing the native flora. Its spread poses a threat to the survival of some of these endemic species.

Impact on humans and related activities
In Fiji the invasion of pasture land made livestock farming uneconomic in places and also provided an excellent breeding ground for insect pests. Despite the fruit's food value, it is considered a pest. In many regions it supplies valuable firewood and is a good food source.

Control
In the Galapagos restriction to cattle movement is the main factor which can slow the spread of the invasion both by preventing the dispersal of seeds and the production of regeneration sites. Established trees are cut and stumps painted with herbicide. In Fiji *P. guajava* has been most successfully controlled from arable land using mechanical means.

Ecological differences

Existence of ecological equivalent species and competitive interactions in invaded regions
In the Galapagos most native tree species lack VA mycorrhizal associations and their existence in *P. guajava* may give it some competitive advantage. The introduced cattle facilitate the spread and regeneration of the invader but not that of endemic species. Some endemic and rare taxa have failed to regenerate following bush fires whereas *P. guajava* shows a high degree of survival and regeneration.

Differences in status and ecology between invaded and native ranges
The spread in open areas is similar in both native and invaded ranges, however the ability to invade disturbed forest and dominate the native species is only observed on the Galapagos Islands.

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Pierre Binggeli

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Schinus terebinthifolius Raddi (Anacardiaceae)

A South American tree introduced to Florida and Hawai'i for ornamental purposes. In Florida, it started to spread rapidly in the 1960s on abandoned agricultural land and is a threat to parts of the Everglades National Park.

Species characteristics

Life form, size, lifespan

Evergreen tree to 12 m with a broad canopy.

Taxonomy, variation and plasticity

Four varieties have been recognized.

Reproductive biology

Numerous white or yellowish flowers are born on panicles and are insect pollinated. In Florida flowers are pollinated by a native syrphid fly. The tree is dioecious. The drupe, when mature, is bright red and ca. 5 mm in diameter. In Florida robins (*Turdus migratorius*) are the main dispersal agent but introduced bird species also disperse the fruits. It produces fruits in its second year. Flowering occurs synchronously in October and fruits mature between December and January, although some reproductive activity may occur throughout the year.

Resilience and resistance

The species sprouts after fire and is resistant to salt-spray. It possesses mycorrhizal associations. It is thought to release allelopathic chemicals.

Environmental requirements and successional status

In abandoned farmland of Florida *S. terebinthifolius* is last species to become established in secondary succession and its stands are self-maintaining. Seedlings become established and survive both in open areas and under dense canopies.

Products and uses

Fruit-laden branches are used as Christmas decorations in both Hawai'i and Florida and the tree is sometimes known as the Christmas berry. It is an important winter ornamental in Florida.

Status in native range

Range and abundance

Native to Brazil, Paraguay and northern Argentina where it is sparsely distributed.

Climate

Dry tropical and sub-tropical regions of South America.

Site requirements

Grows in a variety of habitats from coastal areas behind the mangrove fringe to around 700 m a.s.l. Favours disturbed habitats such as riverine forests.

Weediness

Not reported.

Pests and diseases

A number of insect species feeding on *S. terebinthifolius* have been recorded in Brazil.

Status in invaded regions

History of introductions and intensity of invasions

Introduced to Hawaii as an ornamental before 1900 and to Florida in 1989. In Florida it was first collected in the 1840s but was not widely planted until the 1920s and only became a conspicuous component of natural vegetation in the 1960s. It often forms monotypic stands.

Patterns of invasion and time-lag

In Florida *S. terebinthifolius* invades coastal and mesic prairies, pineland and particularly abandoned agricultural land where stem densities of up to 11355 stems ha-1 have been recorded. However, it is not found in areas were flooding lasts longer than 3-6 months. In pinelands *S. terebinthifolius* is largely excluded by fire when fire occurs in 3 to 7 year cycles. Successful establishment is lower in wetter areas probably as a result the elimination of and/or changes in the mycorrhizal associations. After the abandonment of farmland the *S. terebinthifolius* rate of spread increased dramatically as a result of soil improvement caused by increased nutrients and increased limestone pulverized from the bedrock during ploughing.

Site and climate

In Hawai'i it invades low-lying rangelands and waste grounds that receive a mean annual rainfall of 500 to 1150 mm. In Florida the rainfall is around 1600 mm with rains concentrated between May and October. Occasional winter frosts occur.

Floristic region and vegetation types

In Hawai'i it is found in coastal dry forest dominated by a mixture of exotics. The Everglades National Park contains a large number of tropical plants as well as 65 taxa endemic to southern Florida but is susceptible to invasive woody plants.

Pests and diseases

Cassytha filiformis, a parasitic climber native to Florida, has recently been found to significantly limit foliage production and reproductive capacity of *S. terebinthifolius*.

Impact on ecosystem
It alters successional patterns. In the Everglades, following farming that improves site quality, a forest community dominated by *S. terebinthifolius* replaces herbaceous plant communities. The intertwining crowns create dense shade resulting in little understorey herbaceous vegetation. This lack of vegetation and the limited leaf litter (leaves decompose rapidly) reduce fire susceptibility in mature stands. A number of wintering birds feed on the berries including introduced species.

Impact on humans and related activities
It has no forage value and where it forms dense canopies it shades out desirable forage grasses. Skin contact with leaves and the milky sap results in red, itching rashes and the tree's allergens also cause respiratory difficulties in many people. Profuse regeneration in suburban areas is not welcomed.

Control
Three insect species were introduced from Brazil to Hawaii in the 1950s to control *S. terebinthifolius*. By the mid 1960s the tree was only partially controlled on Hawai'i. On abandoned farmland infested by *S. terebinthifolius*, repeated burning does not retard or reduce the growth of mature trees but has some impact on smaller individuals. Fire is not considered as an appropriate management tool. Control using chemical and mechanical treatments, removal of substrate and particularly flooding has been used. Wetland restoration has been the most successful method used in controlling the spread of the species.

Ecological differences

Existence of ecological equivalent species and competitive interactions in invaded regions
No native species appears to be able to take advantage of soil changes induced by past farming practices, particularly in relation to mycorrhizal associations. Under these conditions *S. terebinthifolius* clearly outcompetes native species. Its reproductive phenology differs markedly from native species with flowering in autumn and the production of ripe fruits in winter.

Differences in status and ecology between invaded and native ranges
The introduction of insects for biological control suggest that the impact of insects on *S. terebinthifolius* populations is absent or negligible in the invaded range but has some impact in its native range.

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Pierre Binggeli

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Ulex europaeus L. (Papilionaceae)

Evergreen shrub from the Atlantic margin of Europe introduced to and spreading in many parts of the world. In the tropics it forms monotypic stands in mountainous areas subjected to large herbivore disturbance and/or fire.

Species characteristics

Life form, size, lifespan

Much-branched evergreen shrub to 2-4 m tall.

Taxonomy, variation and plasticity

In SW Britain *U. europaeus* hybridizes with *U. galli* Planch. where their flowering periods may overlap. It exhibits much intra- and inter-population variation in morphology. Leaves are present only at the seedling stage but thereafter are replaced by spines or scales.

Reproductive biology

The hermaphrodite yellow flowers are usually insect-pollinated and 1 to 3 of them are bone on axillary clusters. Pods (2 cm long) open explosively releasing 2 to 6 seeds and the seeds (6.2 mg, 3.3 x 2.3 mm) may be further dispersed by ants. Seeds can germinate after been subjected to temperature up to 88°C. A persistent seed bank is formed as some seeds remain viable for up to 28 years in the soil. In Britain flowering time varies from January to May according to latitude and set seeds two months later. Seed germination and seedling survival is lower under a *U. europaeus* canopy than in the open.

Resilience and resistance

When cut it coppices freely and following fire seed germination leads to high densities of seedlings. Shoot layering occurs. The species forms nitrogen-fixing root nodules. Its rooting system is shallow with a deep tap root.

Environmental requirements and successional status

Seedlings are often found at sites with some bare ground. Its nitrogen fixing capacity allow growth under conditions of extreme infertility. The shrub is light demanding and dies through shading but seedlings may become established under its own canopy. Bushes start degenerating after 20 years unless fire occurs.

Products and uses

It has potential for land reclamation and has been used as a hedge plant and for binding soil on dry sandy banks. On marginal land it is a source of food for cattle and ponies and formerly, after removal of spines, it was used for fodder.

Status in native range

Range and abundance

Extensively distributed in the Atlantic part of Europe. Scattered throughout central Europe where it is thought to be naturalised. Rarely found in forests apart from forest edges. May form monotypic stands in disturbed areas.

Climate

Temperate oceanic climate with mild winters and mild to cool summers.

Site requirements

Requires disturbance, such as fire or large grazing herbivores, for establishment. Absent from arable and wetland habitats.

Weediness

Very common in disturbed habits such as wasteland, river banks, quarry spoils, roadsides and railway embankments. Has increased since the 1950s after myxomatosis dramatically reduced rabbit populations.

Pests and diseases

A large number of insects have found feeding on the shrub, but at very low densities.

Status in invaded regions

History of introductions and intensity of invasions

Introduced to many montane regions of the tropics, including Peru, La Réunion, Sri Lanka, St Helena and Hawai'i. *U. europaeus* is now naturalized in Sri Lanka and is considered a serious pest on two Hawaiian Islands. It was inadvertently introduced prior to 1910 when the wool industry was established. The species was introduced to many temperate regions and is a serious pests. In La Réunion it has extensively invaded heathlands, particularly in areas disturbed by cultivation and grazing. It forms monotypic stands in South America including in areas previously forested. Invasive in many temperate areas were the plant was often used as hedge material.

Patterns of invasion and time-lag

U. europaeus forms impenetrable and often extensive thickets with as many as 60,000 stems/ha. Its poor long-distance dispersal ability ensures that few distant founder populations are started. During the 1930s Hawaiian ranchers converted to cattle ranching and *U. europaeus*, until then controlled by sheep grazing, began to increase. Microsites produced by the hooves of large herbivores are ideal for gorse seedling establishment, gorse being a poor competitor. Drought and associated removal of grazing pressure appear to have contributed to the infestations.

Site and climate

It grows as low as 460 m a.s.l. but most of its distribution is between 630 and 2220 m. In South America the shrub is found up to 3200 m.

Floristic region and vegetation types

Range land vegetation often on site of former forests.

Pests and diseases

Not reported but presumably are few and have no significant effect.

Impact on ecosystem

In La Réunion it is said that *U. europaeus* has a higher combustible biomass and is probably more flammable than the native vegetation. In some parts New Zealand it has been suggested that stands of *U. europaeus* facilitate the regeneration of native forest trees. Its presence results in some soil acidification.

Impact on humans and related activities

U. europaeus represents a fire hazard to private property. It invades watersheds which supply a substantial amount of drinking water. It is threatening agricultural and grazing lands. Thickets are impenetrable to humans and have persistent spiny litter.

Control

In Hawaii, temporary control was undertaken in the 1970s using 2,4-5 T. The ban of the herbicide and lack of funding ended the programme. A task force was later set up to coordinate a management approach which included the following four control programmes: a/ containment: using Tordon 22K strips along roadsides were first targeted to eliminate the possibility of seed transport to new areas, b/ long-term biological: search for control agents in Europe which in 1984 resulted in the release of a seed weevil (*Apion ulicis* Forster). The weevil is now well established and spreading, but despite destroying 50% of seeds it had no detectable impact on the spreading populations c/ reforestation: using mainly native trees to shade out *U. europaeus* and d/ grazing: use of goats (*Capra hircus*) after fire.

Ecological differences

Existence of ecological equivalent species and competitive interactions in invaded regions

No clear evidence is available but it appears that no equivalent species occur in any of the tropical regions invaded.

Differences in status and ecology between invaded and native ranges

Unusual case of a species with a temperate Atlantic distribution invading mountainous tropical regions as well as other temperate regions. However in all reported cases both in native and invaded *ranges U. europaeus* regeneration is highly favoured by the production of microsites by large hoofed mammals, particularly cattle. Differences in seedbank have been found between temperate regions.

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