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An Expert System for Screening Potentially Invasive Alien Plants in South African Fynbos

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The development and application of an expert system is described for screening alien woody plants for their invasive potential in South African fynbos. The system is proposed for use by potential introducers to demonstrate low invasive risk before importing woody alien species for cultivation. Rules for the system were derived from empirical evidence by quantifying invasion windows and barriers that have limited the set of widespread woody invaders (trees and shrubs) in fynbos to fewer than 20, out of several hundred introduced species. The system first compares broad-scale environmental conditions (climate and soil) between the home environment of a species and fynbos. Features of the plant in its home environment (basic life history traits, population characteristics, regeneration biology, habitat preferences) are then assessed. Finally, an assessment is made of life history adaptations to the prevailing fire regime in fynbos (juvenile period, fire-survival capacity of adult plants, seed bank longevity). The reasoning is explicit and the steps leading to a conclusion (high risk/low risk) can be retraced.

Besides the obvious application in identifying species with a high risk of invading, the system has considerable potential for modelling, and for teaching the concepts of biological invasions. The rules provide an explicit conceptualization of invasion processes in fynbos and identify multiple paths to invasive success (not all of which have been realized yet). The system can therefore be used in planning control operations (for optimal allocation of control effort to critical stages in invasion), and for predicting the outcome of changes (e.g. in fire frequency) on the dimensions of invasion windows, and for assessing what changes are needed to prevent or reduce the extent of invasion by a given taxon.

Application of the system is demonstrated on *Pinus* and *Banksia* taxa and a selection of species from Californian chaparral.

Keywords: biological invasions, risk assessment, expert systems, *Banksia*, *Pinus*.

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TABLE 1. Widespread alien plants in fynbos (after Richardson *et al.*, 1992). Extent of invasion is expressed as the percentage of the 198 quarter degree squares in the fynbos biome

No.	Species	Family	Origin	Extent of invasion	Date of introduction
1	*Acacia cyclops*	Fabaceae	Australia	65	1857
2	*Acacia longifolia*	Fabaceae	Australia	42	1827
3	*Acacia mearnsii*	Fabaceae	Australia	47	1858
4	*Acacia melanoxylon*	Fabaceae	Australia	26	1848
5	*Acacia saligna*	Fabaceae	Australia	60	1848
6	*Hakea gibbosa*	Proteacae	Australia	4	1835
7	*Hakea sericea*	Proteacae	Australia	30	1858
8	*Hakea suaveolens*	Proteacae	Australia	?(<5)	c.1850
9	*Leptospermum laevigatum*	Myrtaceae	Australia	10	1850
10	*Paraserianthes lophantha*	Fabaceae	Australia	14	1835
11	*Pinus halepensis*	Pinaceae	Mediterranean Basin	?	1830
12	*Pinus pinaster*	Pinaceae	Mediterranean Basin	30	1680
13	*Pinus pinea*	Pinaceae	Mediterranean Basin	?	?
14	*Pinus radiata*	Pinaceae	California	17	1865

1. Introduction

The spread of alien trees and shrubs is a major problem in fynbos, the natural vegetation of the southern and southwestern Cape Province of South Africa (Richardson *et al.*, 1992). Dense stands of invasive trees and shrubs, notably species in the genera *Acacia*, *Hakea* and *Pinus*, alter many features of invaded ecosystems (Versfeld and van Wilgen, 1986). They suppress indigenous plants, and currently threaten about 750 species with extinction (Richardson *et al.*, 1992). The alien stands have a much greater biomass and leaf area than fynbos and use more water, resulting in reduced stream flow from catchments (Versfeld and van Wilgen, 1986). The altered vegetation structure sometimes leads to more frequent and more intense fires than in uninvaded fynbos (van Wilgen and Richardson, 1985). Fires in dense alien stands are difficult to control and often have detrimental effects on the soil and native biota. Alien plants also reduce the aesthetic value of fynbos. The control of existing dense stands of alien plants forms a major part of management action in mountain catchments and nature reserves in fynbos (van Wilgen *et al.*, 1992).

The most widespread invasive trees and shrubs in fynbos were introduced intentionally from mediterranean-climate regions on other continents to provide timber or fuel, for drift sand stabilization, or for aesthetic purposes. All the major woody invaders in fynbos (Table 1) were introduced to the region before 1870 and most have been widely planted (Richardson *et al.*, 1992). Several hundred species introduced at about the same time as these invaders and planted fairly extensively have not invaded or are much less widespread. Even within the genera *Hakea* and *Pinus*, which are well represented in the invasive flora, some species have failed to invade or are much less widespread than others (Richardson *et al.*, 1994). The differential success of introduced species as invaders provides a useful natural experiment for deriving empirical evidence on the factors that determine whether an introduced species will invade fynbos or not, or to what extent (Richardson and Cowling, 1992). This evidence can be used to derive procedures for determining, or at least ranking, the invasive potential of new arrivals

(Richardson *et al.*, 1990). New species are still being introduced for forestry, horticulture and other purposes, and effective screening will reduce the problem of invasive plants in the future.

Swarbrick (1991) stressed the need for a rating scheme for environmental weeds. Aggressiveness and potential impact are suggested as the dominant factors, and five classes of weeds were proposed. The most serious class, "canopy dominant", includes species capable of totally dominating the receiving community, replacing its canopy and altering its structure and functioning. The other extreme is represented by "minor weeds" which do not dominate or significantly affect the target environment, and "ruderal" weeds which only invade recently disturbed areas and do not persist when more stable vegetation becomes established. The categories may be expanded to indicate life form, importance, or other attributes. For example, *Pinus radiata* might be classified as 1*tv*—a canopy dominant (class 1) tree (*t*) with visual impact (*v*) on the invaded community.

This paper considers only Swarbrick's first category, which comprises the most serious invaders of fynbos. We assess invasion potential only for fynbos vegetation, and not for many other vegetation types and man-modified habitats that are embedded in the matrix of vegetation formations in the fynbos biome (see Cowling and Holmes, 1992; see also Discussion). Several of the most widespread woody invasive alien species in fynbos are concentrated in riparian habitats. These habitats are severely invaded throughout the world, and the determinants of invadability have been well studied (e.g. Pyšek and Prach, 1993). We do not consider these habitats here.

We describe the development and application of an expert system for screening alien plants to determine the risk of them invading fynbos and becoming canopy dominant weeds.

2. Methods

2.1. Identification of barriers and invasion windows and the formulation of queries and rules

The expert system described here is an extension of the work by Richardson *et al.* (1990), Richardson and Cowling (1992) and Richardson *et al.* (1992). Using theoretical argument and empirical analyses, these authors developed a protocol for risk assessment based on characteristics of the fynbos environment and biological profiles of successful invaders. The approach involves conceptualizing the processes involved in the invasion of fynbos by alien plants in the form of a flow diagram. The salient components that characterize potential barriers to an introduced plant, or, when conditions are beneficial, "invasion windows" (*sensu* Johnstone, 1986), are thus identified. The original papers cited above provide details of the rationale for this approach.

Our starting point was the flow diagram of risk assessment proposed by Richardson and Cowling (1992). The final flow diagram, the queries and the rules for the expert system were generated by repeatedly tracing the paths of known invaders and failed introductions through the flow diagram and making changes where necessary. Experts were regularly consulted for comment on the system as a whole, and on certain aspects within their particular areas of expertise (e.g. soil chemistry, biological control).

2.2. Implementation

The expert system was developed using **DmX**, a development shell featuring exhaustive forward and backward chaining inference mechanisms and comprehensive truth-maintenance facilities (Decision Management Software, 1990). An *explain* facility is provided to enable users to query how the system reached a particular conclusion during the inference process. Inferences are implemented with MYCIN-like (Shortliffe, 1976; Buchanan and Shortliffe, 1984) backward-chaining (see Jackson, 1990; Rich and Knight, 1991). Searching is strongly constrained to conform to the flow diagram by assigning suitable costs to the windows associated with the questions, and through use of the conventional procedural features of the language provided with the development shell.

2.3. USING THE EXPERT SYSTEM

The system was designed for use by ecologists with a good knowledge of fynbos and the concepts of biological invasions. Some of the questions require detailed knowledge of life history attributes of the species and the characteristics of its home environment, some of which can be gleaned from the literature. The user is first required to enter the name of the species to be screened and to check fynbos default values for the typical fire return time, the minimum fire return time and the minimum annual rainfall. The system then queries the user to ascertain whether the species can be dismissed as low risk in terms of any of the invasion barriers. When a classification is made, the system displays the result and allows the user to exit, ask for explanations, or retrace the steps leading to that categorization.

Due to uncertainties inherent in the ecology of biological invasions (Richardson and Cowling, 1992 and references therein), the system is explicitly conservative. A species is assigned high-risk status unless there is sufficient evidence that it has a very low likelihood of invading. Where applicable, if the user responds "unknown" to a question, that query is not taken into account, and control is transferred to the next module on the route to "high risk" status. Therefore, absence of information does not bias assessments towards "low risk" status.

2.4. APPLICATIONS

The system was first used to show how the species that have already invaded fynbos (Table 1) overcame the various barriers to invasion and/or exploited invasion windows (i.e. to identify the routes they have taken through the flow diagram). Assessments were also made of a range of alien plant species which have not yet been introduced, or which have been introduced but have not yet shown signs of invading fynbos (Table 2).

3. Results

3.1. IDENTIFICATION OF INVASION WINDOWS AND THE FORMULATION OF QUERIES AND RULES

The final flow diagram for assessing the risk of invasive success of introduced trees and shrubs in fynbos comprised 24 questions (Appendix 1) which are grouped into six modules—the rectangles in Figure 1. The queries in these modules and the different routes to low and high risk status are shown in Figures 2–7.

TABLE 2. Alien species not yet introduced (or only recently introduced) to the fynbos biome, but which are likely to be introduced soon (or propagated in greater numbers). Suffixes -c, -l and -m for *Pinus contorta* represent the varieties *contorta*, *latifolia* and *murrayana* respectively. Suffixes -a, and -m for *Banksia meisneri* represent varieties *adscendens* and *meisneri* respectively

Family	Genus	Taxa
Pinaceae	*Pinus*	*albicaulis, aristata, attenuata, balfouriana, banksiana, canariensis, clausa, contorta-c, contorta-l, contorta-m, densiflora, flexilis, gerardiana, koraiensis, lambertiana, leiophylla, muricata, patula, pungens, serotina, sibirica, strobus, virginiana*
Proteaceae	*Banksia*	*attenuata, burdetti, candolleana, coccinea, elegans, hookeriana, laricina, leptophylla, media, meisneri-a, meisneri-m, menziesii, prionotes, quercifolia, scabrella, telmatiaea, tricuspsis, victoriae, violaceae-n*
	Grevillea	*leucopteris*
	Hakea	*salicifolia*
Rosaceae	*Adenostoma*	*fasciculatum, sparsifolium*
Ericaceae	*Arctostaphylos*	*glandulosa, glauca, stanfordiana, viscida*
Asteraceae	*Artemesia*	*californica*
Rhamnaceae	*Ceanothus*	*crassifolius, greggi, leucodermis, megacarpus*
	Heteromeles	*arbutifolia*
	Rhamnus	*californica, croces*
	Rhus	*ovata*

3.2. APPLICATIONS

3.2.1. *Introduced species: current invaders and pines*

The established invaders in fynbos are all classified as high risk (HR1), except for *Acacia mearnsii*, *Paraserianthes lophantha* and *Pinus pinea* (Table 3). Table 4 shows predicted paths for a selection of *Pinus* species (selected from Richardson *et al.*, 1990) which have been introduced to the Cape but which have not yet invaded fynbos.

3.2.2. *Potential introductions*

Richardson *et al.* (1990) identified *Banksia* (Proteaceae) as a genus with many species that were likely to be introduced to fynbos because of their commercial potential in the cut-flower market (Burgman and Hopper, 1982). Predicted paths for a selection of *Banksia* taxa previously assessed by Richardson *et al.* (1990) are shown in Table 5. Three taxa listed in Table 5 (*Banksia coccinea*, *B. hookeriana* and the shrub form of *B. menziesii*) were recently introduced (Richardson *et al.*, 1990).

Table 6 shows predicted paths for a selection of Californian chaparral species, and a few other species of interest. Apart from *Heteromeles arbutifolia*, *Rhus ovata*, *Rhamnus californica* and *R. croces*, which are classified as high risk, the chaparral species were all classified as low risk (LR3).

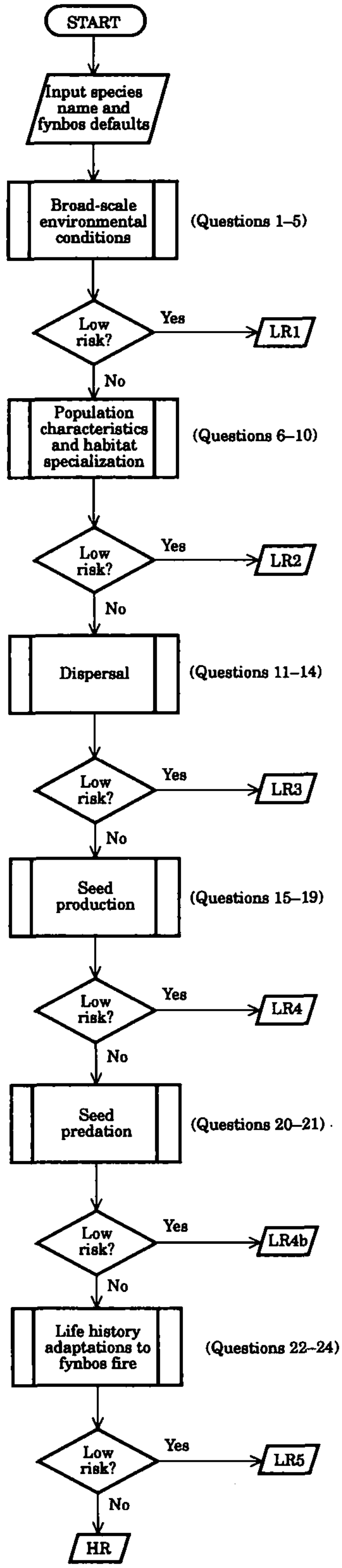

Figure 1. Modules of the expert system for assessing the invasive potential of introduced plants in South African fynbos. The output symbols (small parallelograms) indicate "display risk status" and either "exit" or "explain". Details of the queries within each module (the rectangles) are given in Figures 2–7. The relevant questions (and rationale where appropriate) are given in Appendix 1. Details of the rules for assigning risk are given in Appendix 2.

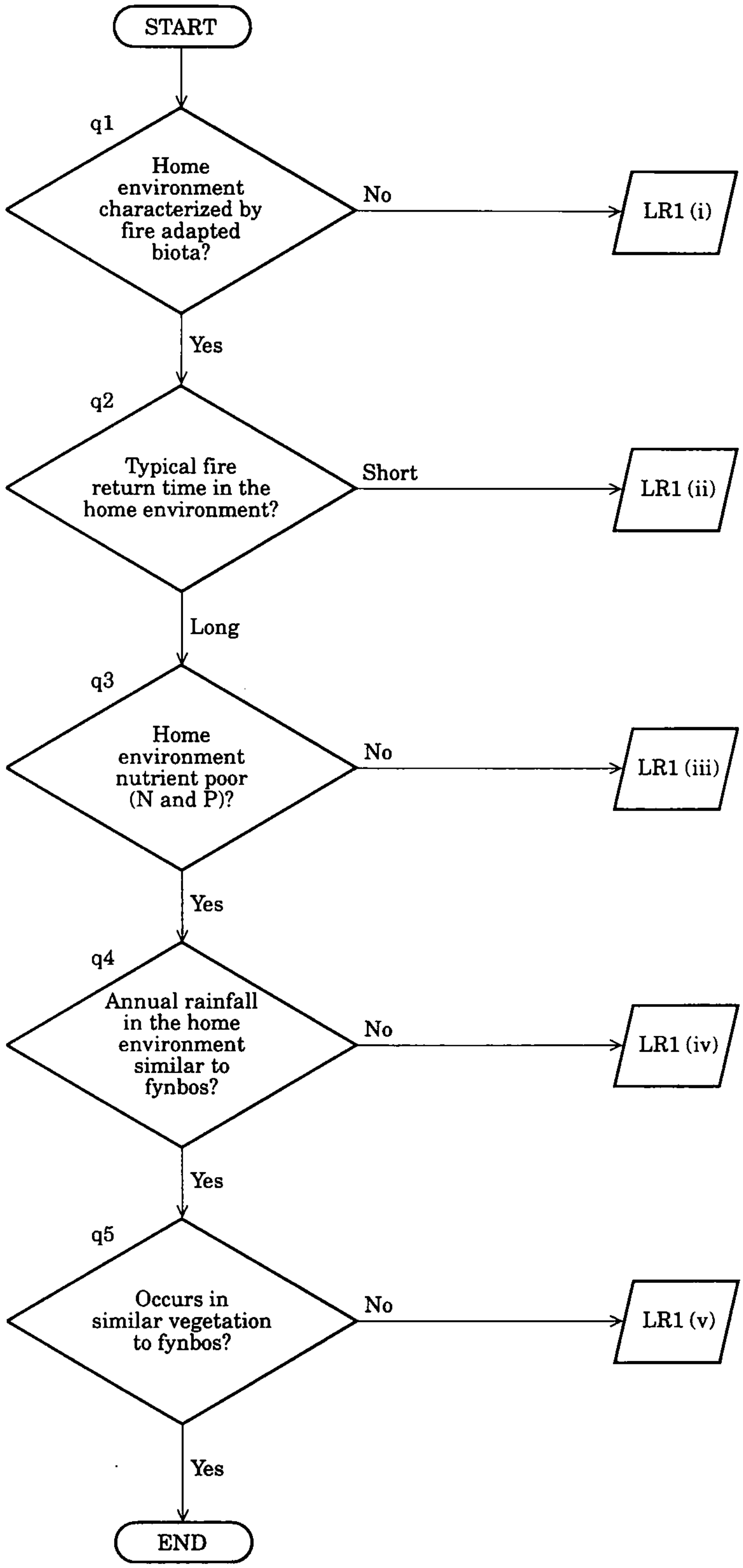

Figure 2. Queries pertaining to broad-scale environmental conditions (q1–q5 refer to Questions 1–5 in Appendix 1).

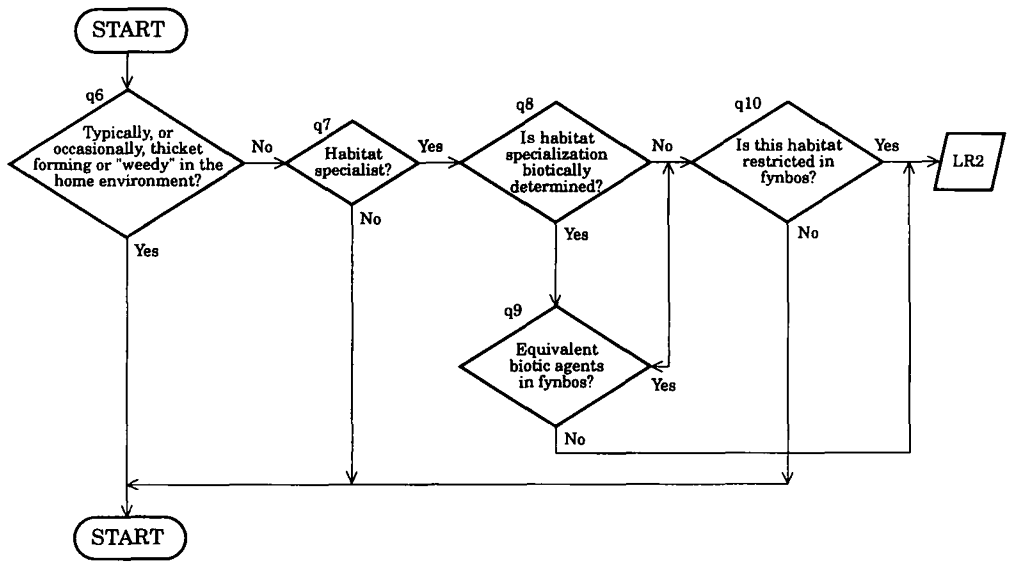

Figure 3. Queries pertaining to population characteristics and habitat specialization (q6–q10 refer to questions 6–10 in Appendix 1).

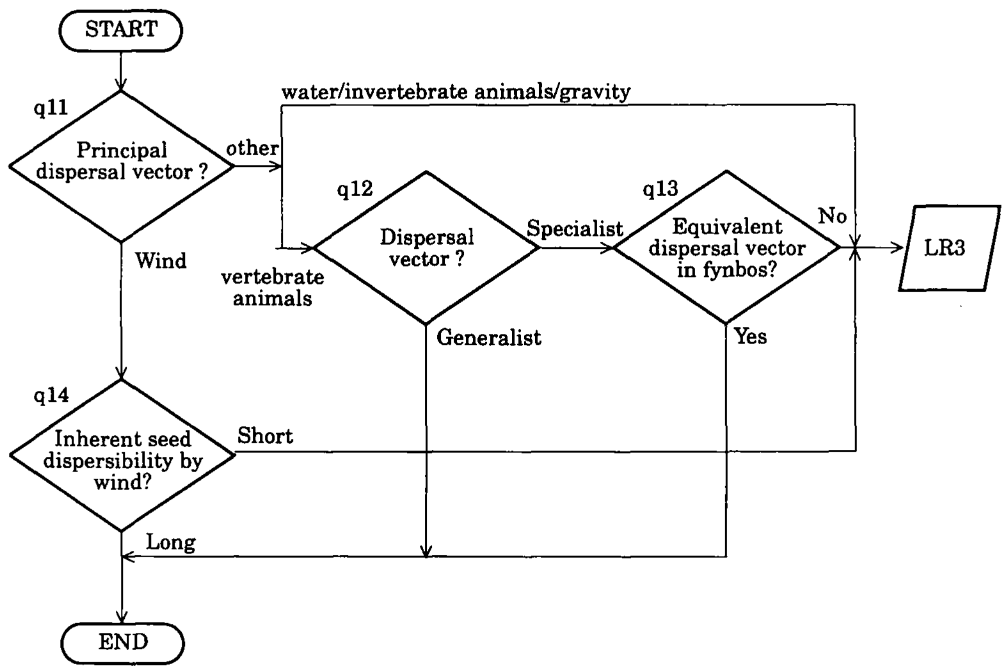

Figure 4. Queries pertaining to seed dispersal (q11–q14 refer to questions 11–14 in Appendix 1).

4. Discussion

4.1. IDENTIFICATION OF BARRIERS AND INVASION WINDOWS AND THE FORMULATION OF QUERIES AND RULES

The iterative process of developing the expert system provided new insights that

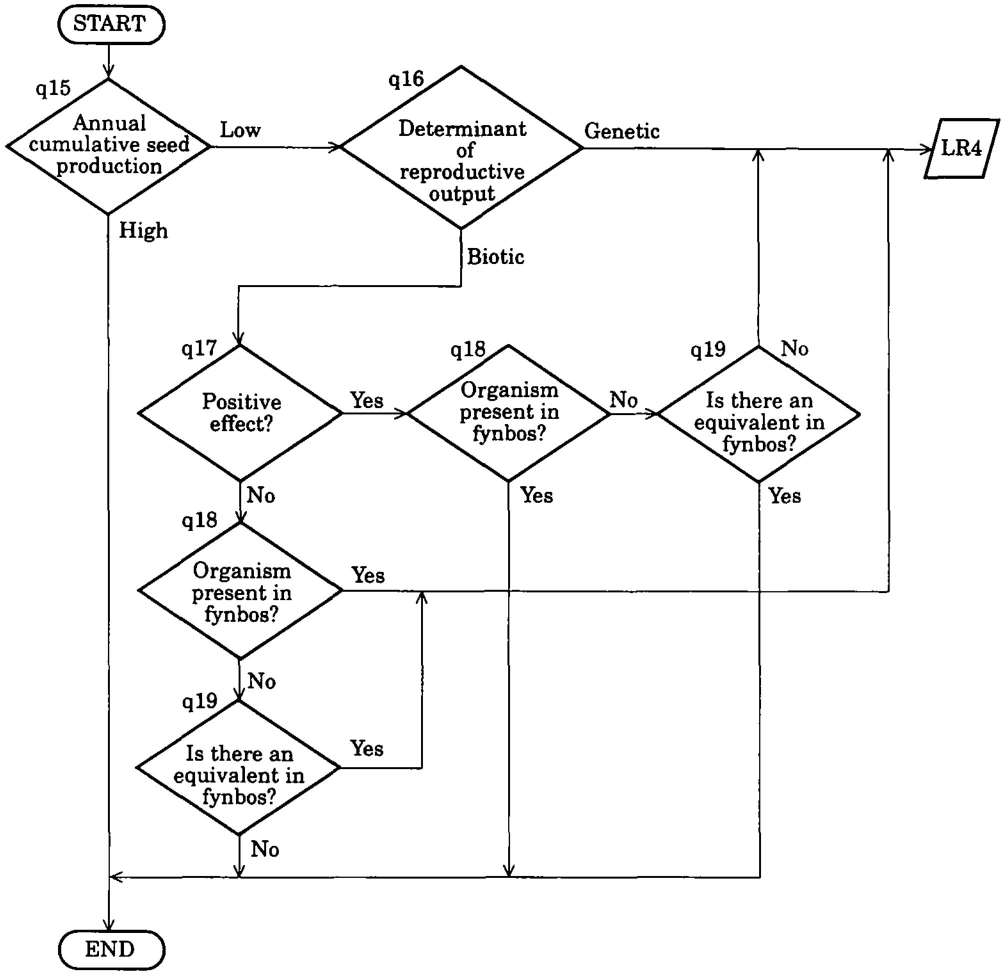

Figure 5. Queries pertaining to seed production (q15–q19 refer to questions 15–19 in Appendix 1).

facilitated modifications and refinements to the original protocol of risk assessment proposed by Richardson and Cowling (1992). Modifications included a more detailed consideration of the broad-scale environmental conditions of the home environment (Figure 2), the role of biotic agents in determining habitat specificity for the "non-weedy" species (Figure 3), and the potential role of dispersal vectors other than wind (Figure 4). The section on seed production was refined to accommodate fynbos equivalents of the biotic determinants of reproductive output which have a negative effect in the home environment (Figure 5). The underlying assumptions of the risk assessment model of Richardson and Cowling (1992) are retained in the expert system.

Two implicit assumptions were called into question during analyses of pines and banksias, and deserve mention here. The first is that the attributes of a taxon remain the same after introduction. Some attributes used in risk assessment may vary across the range of a species, and may change markedly when the species is cultivated. For example, the juvenile period of *Banksia candolliana* may drop from 15 years in its natural environment to 5 years in cultivation; and *Banksia leptophylla* produces few

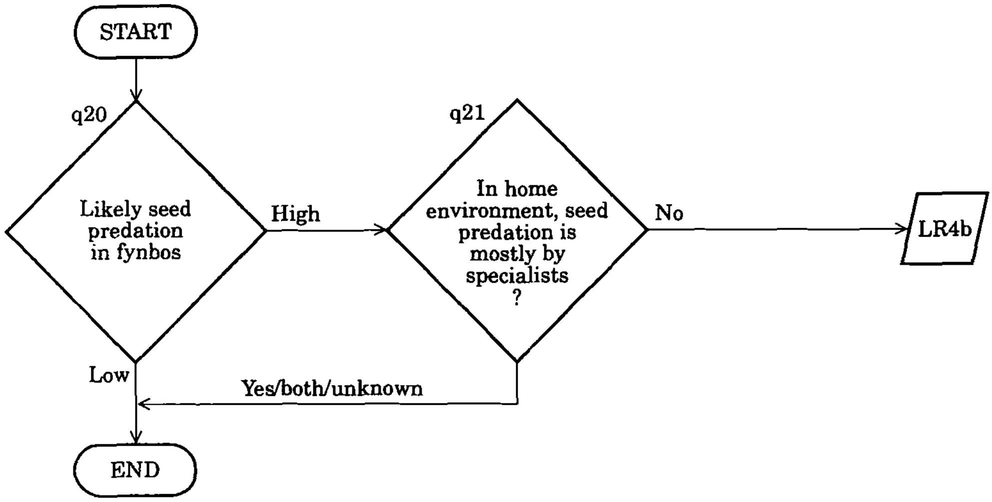

Figure 6. Queries pertaining to seed predation (q20–q21 refer to questions 20–21 in Appendix 1).

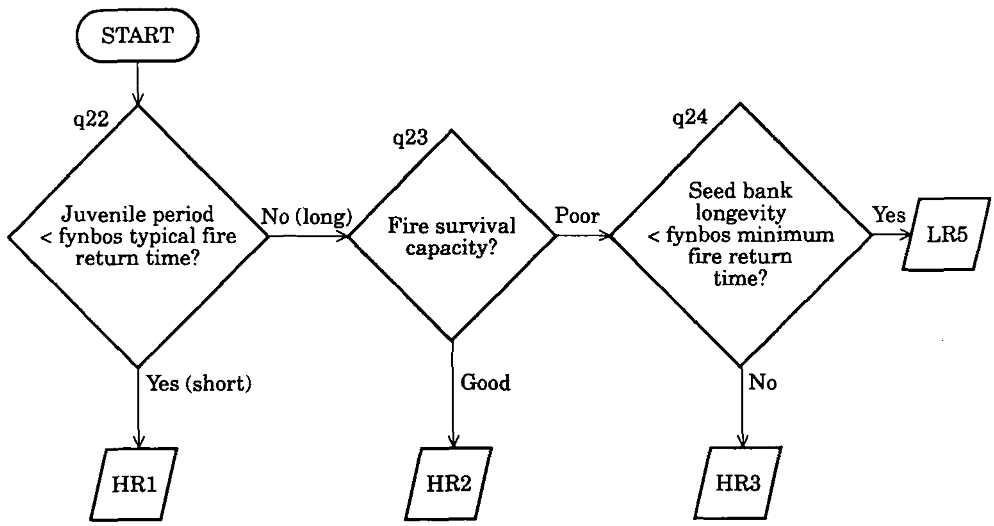

Figure 7. Queries pertaining to life history adaptations to fynbos fire (q22–q24 refer to questions 22–24 in Appendix 1).

seeds in cultivation (B. B. Lamont, personal communication). Species classified as "high risk" are from environments similar to fynbos and such effects are unlikely to be important in screening for invasive potential.

The second assumption concerns factors determining species distributions and other attributes in the home environment. In their analysis of invasive pines in fynbos, Richardson and Cowling (1992) concluded that factors restricting *Pinus halepensis* and *P. pinaster* to specific (and separate) sites in the Mediterranean Basin do not operate in fynbos. Such conclusions are only possible *after* introduction and establishment, and the precise factors and subtle interactions involved cannot be determined *a priori.* For

TABLE 3. Current invaders and their paths to high risk status. Species numbers correspond with those in Table 1. Abbreviations: ? = unknown; DF = dry forest; GEN = generalist; GR = gravity; GTC = genetic; Hi = high; II = isolated individuals; Lo = low; LW = low woodland (here taken as functionally equivalent to dry forest); MED = medium; MDT = Mediterranean-type shrubland; N = no; OW = occasionally weedy; SP = specialist; VER = vertebrate; WAT = water; WDY = weedy; WND = wind; Y = yes. An empty cell in the table, or a value in square brackets, indicates that the system did not ask that question during screening of that species. Most responses in Table 3 were based on information in Richardson *et al.* (1992). Major sources of information for pines were: Richardson (1988); Richardson and Bond (1991); Richardson *et al.* (1990) and Richardson and Brown (1986). Primary sources for *Hakea* were: Kluge and Neser (1991) and Richardson and Cowling (1992); B. B. Lamont provided additional information for *H. suaveolens*. Information on *Leptospermum laevigatum* is from Molnar *et al.* (1989)

Species	Question numbers																								
no.	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	17	18	19	20	21	22	23	24	Outc
1	Y	?	Y	?	MDT	WDY					VER	GEN			Hi					Hi	both	3			HR1
2	Y	?	Y	?	DF	WDY					VER	GEN			Hi					Hi	both	3			HR1
3	Y	?	Y	?	DF	WDY					WAT														LR3
4	Y	?	Y	800	DF	WDY					VER	GEN			Hi					Lo		3			HR1
5	Y	?	Y	?	MDT	WDY					VER	GEN			Hi					Hi	both	3			HR1
6	Y	15–20	Y	800–1500	DF	II	N				WND			Y	MED					Lo		2			HR1
7	Y	15–20	Y	800	DF	OW					WND			Y	Hi					Lo		2			HR1
8	Y	?	Y	650	MDT	WDY					WND			Y	MED					Lo		4			HR1
9	Y	?	Y	725	MDT	WDY					WND			Y	Hi					Lo		5			HR1
10	N																								LR1
11	Y	15	Y	600	DF	WDY					WND			Y	Hi					Lo		15	Good		HR2
12	Y	15	Y	500	DF	WDY					WND			Y	Hi					Lo		6			HR1
13	Y	15	Y	700	DF	OW					VER	SP	N		[Hi]					[Lo]		[15]	[Poor]	[short]	LR3
14	Y	15	Y	600	DF	WDY					WND			Y	Hi					Lo		9		[5]	HR1

TABLE 4. Paths for selected *Pinus* species. See Table 3 for abbreviations. Primary sources of data were: Richardson *et al.*, 1990; Richardson and Bond, 1991; Richardson and Cowling, 1992. Vertebrate dispersers in the home environments were assumed to be generalists (Question 12 in Appendix 1). Seeds were assumed to be structurally adapted for "long" wind dispersal if the seed-wing areas listed in Richardson *et al.* (1990), are greater than 50 mm^2 (Question 14 in Appendix 1). The juvenile periods are minimum juvenile periods listed and referenced in Richardson *et al.* (1990). Provided a species is not excluded on criteria considered earlier, a juvenile period of less than 12 years (the fynbos default fire-return time) results in a high risk (HR1) classification. Fire survival capacity is "poor" if the fire tolerance index is 0 (thin bark), otherwise it is rated as "good" (Question 23) (cf. Richardson *et al.*, 1990). All are assumed to be "weedy" in their home environments although an "unknown" response would lead to the same conclusion in every case. The questions are listed in Appendix 1.

	Question numbers																							
Pinus taxon	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	17	18	19	20	21	22	23	24	Risk
albicaulis	Y	?	Y	?	DF	WDY					VER	GEN			?					Lo		20	Poor	?	HR3
aristata	Y	?	Y	?	DF	WDY					WND			Y	?					Lo		20	Good		HR2
attenuata	Y	?	Y	?	DF	WDY					WND			Y	Hi					Lo		5			HR1
balfouriana	Y	?	Y	?	DF	WDY					WND			Y	?					Lo		20	Good		HR2
banksiana	Y	?	Y	?	DF	WDY					WND			Y	Hi					Lo		3			HR1
canariensis	Y	?	Y	?	DF	WDY					WND			Y	?					Lo		15	Good		HR2
clausa	Y	?	Y	?	DF	WDY					WND			Y	Hi					Lo		5			HR1
contorta-c	Y	?	Y	?	DF	WDY					WND			Y	Hi					Lo		4			HR1
contorta-l	Y	?	Y	?	DF	WDY					WND			Y	Hi					Lo		5			HR1
contorta-m	Y	?	Y	?	DF	WDY					WND			Y	Hi					Lo		6			HR1
densiflora	Y	?	Y	?	DF	WDY					WND			Y	?					Lo		20	Poor	?	HR3
flexilis	Y	?	Y	?	DF	?					VER	GEN			?					Lo		20	Good		HR2
gerardiana	Y	?	Y	?	DF	?					WND			Y	?					Lo		28	Poor	?	HR3
koraiensis	Y	?	Y	?	DF	WDY					VER	GEN			?					Lo		15	Poor	?	HR3
lambertiana	Y	?	Y	?	DF	WDY					VER	GEN			?					Lo		40	Good		HR2
leiophylla	Y	?	Y	?	DF	?					WND			Y	?					Lo		28	Good		HR2
muricata	Y	?	Y	?	DF	WDY					WND			Y	Hi					Lo		5			HR1
patula	Y	?	Y	?	DF	WDY					WND			Y	Hi					Lo		10			HR1
pungens	Y	?	Y	?	DF	WDY					WND			Y	Hi					Lo		5			HR1
serotina	Y	?	Y	?	DF	WDY					WND			Y	Hi					Lo		4			HR1
sibirica	Y	?	Y	?	DF	?					VER	GEN			?					Lo		25	Poor	?	HR3
strobus	Y	?	Y	?	DF	?					VER	GEN			?					Lo		5			HR1
virginiana	Y	?	Y	?	DF	WDY					WND			Y	Hi					Lo		5			HR1

TABLE 5. Paths for selected species of *Banksia*. See Table 3 for abbreviations. Suffixes -a and -m for *Banksia meisneri* represent the varieties *ascendens* and *meisneri* respectively. *Banksia violacea-n* is the non-sprouting form of *Banksia violacea*. B. B. Lamont supplied responses for *Banksia attenuata*, *B. burdetti*, *B. candolleana*, *B. hookeriana*, *B. laricina*, *B. leptophylla*, *B. menziesii* and *B. prionotes*. The original responses given were not strictly adhered to as some of the questions were reworked as development of the system progressed. For the other *Banksia* species, information was derived from the data tabulated and referenced in Richardson *et al.* (1990). The questions are listed in Appendix 1.

Banksia taxon	Question numbers																								
	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	17	18	19	20	21	22	23	24	Risk
attenuata	Y	10–20	Y	450–1000	MDT,DF	WDY	[Y]	[N]			WND			Y	Lo	GTC					[SP]	[20]	[Good]	[15]	LR4
burdetti	Y	10–20	Y	550	MDT	OW	[Y]	[N]			WND			Y	Med					Lo		5	[Poor]	[10]	HR1
candolleana	Y	10–20	Y	500	MDT	WDY	[Y]	[N]			WND			Y	Lo	GTC					[SP]	[15]	[Good]	15	LR4
coccinea	Y	10–20	Y	400–1000	MDT	WDY					WND			Y	Hi					Lo		1–5			HR1
elegans	Y	10–20	Y	400–1000	MDT	?					WND			?	Lo	GTC						[6]			LR4
hookeriana	Y	10–20	Y	500	MDT	WDY	[Y]	[N]			WND			Y	Med	[GTC]				Lo		5	[Poor]	[10]	HR1
laricina	Y	10–20	Y	600	LW	OW	[Y]	[N]			WND			Y	Med	[GTC]				Lo	[SP]	5	[Poor]	[10]	HR1
leptophylla	Y	10–20	Y	450-650	MDT,LW	WDY	[Y]	[N]			WND			Y	Med	[GTC]				Lo		5	[Poor]	[15]	HR1
media	Y	10–20	Y	400–1000	MDT	WDY					WND			Y	Hi					Lo		5–10			HR1
meisneri-a	Y	10–20	Y	400–1000	MDT	WDY					WND			Y	Hi					Lo		5–10			HR1
meisneri-m	Y	10–20	Y	400–1000	MDT	WDY					WND			Y	Hi					Lo		5–10			HR1
menziesii	Y	10–20	Y	450–1000	MDT,DF	II	Y	N		?				Y	Lo	GTC					[SP]	[20]	[Good]	[5]	LR4
prionotes	Y	10–20	Y	450–1000	MDT,LW	WDY	[Y]	[N]						Y	Med	[GTC]					[SP]	5	[Poor]	[10]	HR1
quercifolia	Y	10–20	Y	400–1000	MDT	WDY					WND			Y	Hi					Lo		5–10			HR1
scabrella	Y	10–20	Y	400–1000	MDT	WDY					WND			Y	Hi					Lo		1–5			HR1
telmatiaea	Y	10–20	Y	400–1000	MDT	WDY					WND			Y	Hi					Lo		1–5			HR1
tricuspis	Y	10–20	Y	400–1000	MDT	?					WND			Y	Lo	GTC						[20]			LR4
victoriae	Y	10–20	Y	400–1000	MDT	WDY					WND			Y	Hi					Lo		1–5			HR1
violacea-n	Y	10–20	Y	400–1000	MDT	WDY					WND			Y	Hi					Lo		1–5			HR1

TABLE 6. Classifications of chaparral species and others of interest. See Table 3 for abbreviations. Responses for the chaparral species and *Grevillea leucopteris* were provided by J. E. Keeley and B. B. Lamont. The questions are listed in Appendix 1.

	Question number																								
Taxon	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	17	18	19	20	21	22	23	24	Risk
Adenostoma																									
fasciculatum	Y	20–80	?	500	0	WDY	[N]				GR,WND	[N]	[Y]	N	[>500]							[10]	[Good]	[100]	LR3
sparsifolium	Y	20–80	?	400	0	WDY	[N]				GR,WND	[N]	[Y]	N	[>500]							[10]	[Good]	[100]	LR3
Arctostaphylos																									
glandulosa	Y	20–80	?	500	0	WDY	[N]				GR	[N]	[Y]	[N]	[>500]							[10]	[Good]	[100]	LR3
glauca	Y	20–80	?	400	MDT	WDY	[N]				GR	[N]	[Y]	[N]	[>500]							[10]	[Good]	[100]	LR3
stanfordiana	Y	20–80	?	600	MDT	WDY	[N]				GR	[N]	[Y]	[N]	[>500]							[10]	[Good]	[100]	LR3
viscida	Y	20–80	?	600	MDT	WDY	[N]				GR	[N]	[Y]	[N]	[>500]							[10]	[Good]	[100]	LR3
Artemisia																									
californica	Y	20–80	?	300	MDT	WDY	[N]				WND	[N]	[Y]	N	[>500]							[3]	[Good]	[<50]	LR3
Ceanothus																									
crassifolius	Y	20–80	?	500	MDT	WDY	[N]				GR	[N]	[Y]	[N]	[>500]							[10]	[Good]	[100]	LR3
greggi	Y	20–80	?	500	MDT	WDY	[N]				GR	[N]	[Y]	[N]	[>500]							[10]	[Good]	[100]	LR3
leucodermis	Y	20–80	?	500	MDT	WDY	[N]				GR	[N]	[Y]	[N]	[>500]							[10]	[Good]	[100]	LR3
megacarpus	Y	20–80	?	400	MDT	WDY	[N]				GR	[N]	[Y]	[N]	[>500]							[10]	[Good]	[100]	LR3
Heteromeles																									
arbutifolia	Y	20–80	?	400–600	MDT	II	N				VER	N	[Y]	[N]	>500					Lo		10	[Good]	[1]	HR1
Rhus ovata	Y	20–80	?	500	MDT	OW	[N]				VER	N	[Y]	[N]	>500					Lo		10	[Good]	[?]	HR1
Rhamnus																									
californica	Y	20–80	?	500	MDT	OW	[N]				VER	N	[Y]	[N]	>500					Lo		10	[Good]	1	HR1
croces	Y	20–80	?	500	MDT	OW	[N]				VER	N	[Y]	[N]	>500					Lo		10	[Good]	?	HR1
Grevillea																									
leucopteris	Y	10–20	y	400–500	MDT	WDY	[Y]	[N]		?	WND			Y	MED	[GTC]				Lo	[S]	3	[Poor]	[5?]	HR1
Hakea salicifolia	Y	10–20	Y	400–1000	?	OW					WND			Y	Hi					Lo		6			HR1

the purposes of the expert system, it is assumed, where necessary, that such factors *will* apply in fynbos.

4.2. CURRENT INVADERS CLASSIFIED AS LOW RISK

Acacia mearnsii is classified as low risk (LR3, Table 3). Although fairly widespread in the biome (Richardson *et al.*, 1992), it is dispersed by water and tends to be restricted to rivers, streams and ditches and is not a widespread problem in fynbos. Nevertheless, it forms dense impenetrable stands, which suppress indigenous vegetation and reduce stream flow, and thus still adversely affects fynbos. *Paraserianthes lophantha* is also water-dispersed but is assigned low-risk status (LR1i) after Question 1, as fire does not often penetrate riparian habitats in its natural range in Australia. However, like *Acacia mearnsii*, it does invade stream banks and seepages, smothering rare indigenous native species and reducing stream flow.

Riparian habitats throughout the world are invaded by woody plants and the determinants of invadability in these habitats are quite distinct from those of the habitats away from streams (e.g. Pyšek and Prach, 1993). It would be simple to include these determinants in a separate expert system.

The system also assigns *Pinus pinea* low-risk status (LR3), although it has invaded fynbos to a small extent (Richardson and Cowling, 1995). Its better-than-predicted performance in fynbos is attributable to an opportunistic mutualism with the introduced grey squirrel, *Sciurus carolinensis*, which disperses its seeds (Richardson, 1989). Invasions tend to be clustered around stands of the introduced tree, *Quercus robur*, whose acorns form the squirrel's principal food source (Millar, 1980). Such biological interactions may confound the predictions of the system.

The paths to high risk status taken by the other current invaders (Table 3) reflect the invasive functional groups and characteristics of a good invader described by Richardson and co-authors (Richardson *et al.*, 1990, 1992; Richardson and Cowling, 1992, 1993).

4.3. INTRODUCED SPECIES

4.3.1. *Pines*

Most of the pines in Table 4 have been introduced but have been planted on a very small scale, and have not escaped cultivation (Poynton, 1979). The invading pines in fynbos (*Pinus halepensis*, *P. pinaster* and *P. radiata*) belong to a "fire-resilient" group in the genus (cf. McCune, 1988) which is characterized by short juvenile periods and poor fire tolerance. They are strongly serotinous and have small seeds with adaptations for long distance dispersal by wind. They are also not relegated to low risk status on any of the other criteria used by the system: the broad-scale environmental conditions of the home environments are similar to fynbos (Questions 1–4), they occur in vegetation types which are broadly similar to fynbos (Question 5), they tend to be "weedy" in their home environments (Question 6), seed production is likely to be the same or higher in fynbos than in the home environment (Questions 15–19), and seed predation in fynbos is likely to be the same or lower (Questions 20–21). Operational definitions of terms such as "high" and "low" are given in Appendix 1. Based on the above characteristics, the following pines are also classified as high risk species (HR1, Table 4): *Pinus attenuata*, *P. banksiana*, *P. clausa*, *P. contorta* var. *contorta*, *P. contorta* var.

latifolia, *P. contorta* var. *murrayana*, *P. muricata*, *P. patula*, *P. pungens*, *P. serotina*, *P. strobus* and *P. virginiana*.

In the absence of detailed information concerning many of the pines that were considered, the system was unable to classify "low risk" species, as previously identified by Richardson *et al.* (1990), as such. It did, however, distinguish them from the "high risk" pines, which were all classified as HR1, by assigning them HR3 status (*Pinus albicaulis*, *P. densiflora*, *P. gerardiana*, *P. koraiensis*, and *P. sibirica*; Table 4). HR3 is the least worrisome of the high risk categories since taxa thus classified have long juvenile periods and poor fire tolerance. This means that if an individual germinates, it is unlikely to produce seeds before it is killed in the next fire. Persistence relies on its high reproductive output and long distance dispersal abilities facilitating rapid recolonization after fire (e.g. from cultivated stands, or areas where the fire return time has been longer than expected). The final question (Question 24) concerning seed bank longevity was answered "unknown" for all these HR3 species. Distinguishing pre- and post-dispersal longevity with varying seed release strategies remains an area for elaboration. More details of the reproductive output (Questions 15–19) and seed bank longevity (Question 24) of these species are required before their planting can be sanctioned.

A point of departure from the approach of Richardson *et al.* (1990) is the way in which species that are dispersed by generalist vertebrates are categorized. Richardson *et al.* (1990) identified fire-adapted species whose invasive potential in fynbos was "restrained by the requirements for vertebrate dispersal" (e.g. *Pinus flexilis* and *P. lambertiana*). These were regarded as low risk species—the reasoning being that generalist vertebrate seed dispersers are rare in fynbos. The "tightness" of mutualisms which may arise (cf. Redwing starlings and *Acacia longifolia*; see below) are unpredictable, and the expert system makes allowance for opportunistic mutualisms. It does not, therefore, automatically assign low-risk status to species dispersed by generalist vertebrate agents (e.g. *Pinus koraiensis*, *P. lambertiana*, *P. sibirica*, *P. strobus*; Table 4).

The expert system is also more conservative in its classification of some of the group C (low risk) species of Richardson *et al.* (1990). These species possess combinations of traits associated with both high and low risk functional groups. Long juvenile periods are associated with low invasive risk. Where fire survival capacity is "good" the expert system assigns the species high risk status (HR2) provided it has not been excluded on any of the criteria investigated earlier (cf. *Pinus balfouriana*, *P. canariensis* and *P. leiophylla*).

4.3.2. *Hakeas*

The hakea species that have invaded fynbos (*Hakea gibbosa*, *H. sericea* and *H. suaveolens*) share many characteristics with the invading pines and have exploited similar invasion windows to achieve high risk status (HR1, Table 3). The differential invasive success within this genus was attributed mainly to differences in effective reproductive output which influences dispersal ability. *Hakea sericea* produces four and sixteen times as many seeds as *H. gibbosa* and *H. suaveolens*, respectively (Richardson *et al.*, 1987). The prolific seed production of *H. sericea* has enabled it to colonize distant areas not colonized by the other two species (Richardson *et al.*, 1992).

Another species, *Hakea salicifolia*, classified as high risk (HR1, Table 6), has been present in fynbos for more than 100 years but has not invaded. Although it produces large numbers of dispersible seeds, the follicles seem to provide inadequate insulation against the heat of fynbos fires (Richardson *et al.*, 1987).

The path suggests that it would be profitable to enhance the first module (Figure 2) by considering the influence of fire intensity. However, the current version of the system simply assumes that, if fire is characteristic of the home environment, the species has the necessary adaptations to withstand fynbos fires (Question 1, Rule 23). The lack of resolution in this module leads to a conservative high risk classification for borderline cases.

4.3.3. *Acacias*

The invading acacias (*Acacia cyclops*, *A. longifolia*, *A. melanoxylon* and *A. saligna*) are also classified as high risk (HR1, Table 3), but through a slightly different path to that followed by pines and hakeas. Differences in invasive success within this genus are largely attributable to reproductive output. *Acacia saligna* rapidly accumulates large seed banks in the soil. These are persistent due to high viability and water-impermeable dormancy. Seeds are dispersed primarily by ants but also (and further) by water and by birds (Knight and Macdonald, 1991). Rapid germination, cued by fire, accounts for its invasive success (Holmes, 1989). Most of its seed crop is released soon after maturation.

Acacia cyclops also produces large seed banks though these are less persistent than those of *A. saligna*. The seeds are of variable viability and most do not survive a full year. Much of the seed crop is retained in the canopy for several months (O'Dowd and Gill, 1986). The seeds are dispersed by generalist vertebrates (birds) and are able to germinate without having to wait for specific disturbance cues.

Acacia longifolia achieves high risk status along the same path as *Acacia cyclops* and *Acacia saligna*. Although *A. longifolia* is not typically dispersed by birds, dispersal by Red-winged starlings (*Onychognathus morio*) has been a key factor in its success in mountain fynbos (Pieterse, 1986; Richardson *et al.*, 1992). This is another example of an opportunistic mutualism which may confound predictions from empirical models.

Acacia melanoxylon, classified as high risk (HR1), possesses the characteristics required to invade fynbos but it only invades at forest edges and in riparian woodlands. The seeds are primarily dispersed by water and to some extent by birds. The assumption that birds disperse the seeds farther than does water to facilitate invasion results in this (conservative) high risk classification. The question of *how much* seed is dispersed by birds is not addressed. Long established "high risk" species which have not invaded may imply the existence of an unidentified barrier which the other invaders have overcome (e.g. post dispersal environments, dormancy and germination, cf. Keeley, 1991).

4.4. POTENTIAL INTRODUCTIONS

4.4.1. *Banksias*

The high-risk species of *Banksia* in Table 5 correspond with the "invasive" end of the continuum in the correspondence analysis of Richardson *et al.* (1990), where "invasive" and "non-invasive" were used to indicate the two extremes along a gradient of invasive potential. The "invasive" group consists of tall, serotinous species which produce large numbers of well dispersed seeds and have short juvenile periods—attributes instrumental in the success of pines and hakeas (Lamont *et al.*, 1985; Enright and Lamont, 1989*b*; Cowling *et al.*, 1990). The home environment of the *Banksia* species under consideration in southwestern Australia (Taylor and Hopper, 1988), is very similar to fynbos (Cowling *et al.*, 1994). The vegetation of the region is predominantly a fire-prone mediterranean-type shrubland or woodland with a fire-return time varying between 10 and 20 years (Questions 1, 2 and 5). Soils are nutrient-poor (Question 3), and annual rainfall varies between 400 and 1000 mm (Question 4). For many of these *Banksia* species, reproductive output is reduced by specialist insect seed predators which are absent in fynbos. Many species retain their seeds until cool, wet (winter) conditions arise, suitable for germination and establishment. This strategy, not found in fynbos Proteaceae, minimizes post dispersal seed predation irrespective of season of burn (Questions 20–21) (references in Richardson *et al.*, 1990). The expert system classifies thicket-forming species which produce very large viable seed banks such as *Banksia burdetti* (Lamont and Barker, 1988), *B. hookeriana* (Enright and Lamont, 1989*a*) and *B. leptophylla* (Cowling *et al.*, 1987) as high risk (HR1), along with *B. laricina*, *B. prionotes*, *B. coccinea*, *B. media*, *B. meisneri* var *ascendens*, *B. meisneri* var *meisneri*, *B. quercifolia*, *B. scabrella*, *B. telmatiaea*, *B. victoriae* and the non-sprouting form of *B. violacea*.

Richardson *et al.* (1990) note that many of these high-risk *Banksia* species (e.g. *B. coccinea*, *B. hookeriana* and *B. prionotes*) are highly susceptible to infection by the pathogenic fungus *Phytophtora cinnamoni* which attacks their root systems. The expert system does not address the influence of pathogens explicitly, though this effect is incorporated as a determinant of reproductive output by having a negative effect (Questions 15–19) or as effective seed predation (Questions 20–21). In this case, the pathogen may (or may not) attack the root systems at any time rendering prediction of invasibility on this basis unreliable. The fungus is most destructive in plantations and it is not known whether it could check invasions by these species in fynbos.

The "non-invasive" extreme for *Banksia* spp. is characterized by low sprouting shrubs with low reproductive output (cf. Questions 15–19) and long juvenile periods (cf. Question 22) (Richardson *et al.*, 1990). Examples include the widespread shrubs *Banksia menziesii* and *B. attenuata* (Cowling *et al.*, 1987; Enright and Lamont, 1989*b*), *B. elegans* which produces less than one seed per plant on average (Lamont and Barrett, 1988), and *B. tricuspis* which has a juvenile period of at least 20 years (Lamont and van Leeuwen, 1988). All these species are classified as low risk (Table 5).

Although the classifications of the expert system show considerable agreement with the correspondence analyses of Richardson *et al.* (1990), matching categories are not necessarily equivalent. For example, species classified as HR1 do not necessarily correspond fully with the "fire resilient" functional group defined for pines or the "invasive group" for *Banksia*. "Fire-resilient" pines are killed by fire or at least have low fire tolerance. Fire tolerance is not considered in the path to HR1. The height of the plant is also not considered by the expert system when classifying *Banksia* spp. The expert system is only concerned with distinguishing "high risk" from "low risk", and can usually reach a conclusion without requiring a complete set of information on a particular plant.

4.4.2. *Chaparral species*

Adenostoma fasciculatum, *Arctostaphylos* spp. and *Ceanothus* spp. have refractory seeds (fire recruiters *sensu* Keeley, 1991) which do not have specialized structures for long distance dispersal by wind. Question 11 asks for the principle dispersal vector. Where more than one is involved, the user is asked to indicate the one which disperses farthest. *Arctostaphylos* seeds are not fleshy and are not adapted for dispersal by animals. Black bears and coyotes are known to eat the seeds occasionally (Keeley, 1991) but are not regarded as seed predators or dispersal vectors for these species as they have no quantitative impact on the seed crop. Nevertheless, some seeds may pass through intact, facilitating range expansion. This observation would lead to a high risk classification if one considers baboons (*Papio ursinus*) and/or rodents as equivalent generalist dispersal vectors in fynbos. This route is the path to high risk taken by *Heteromeles arbutifolia*, *Rhus ovata*, *Rhamnus californica* and *Rhamnus croces* (Table 6) which are adapted for dispersal by generalist vertebrates (Keeley, 1991).

4.5. COMPARISON WITH OTHER APPROACHES

Various models and rating systems for screening alien species and predicting pest status have been proposed during the last decade and a half (e.g. Weir, 1977; Arthington and Mitchell, 1986; Navarantham and Catley, 1986; Smallwood and Salmon, 1992; Scott and Panetta, 1993). With the exception of Navarantham and Catley (1986), most of the earlier models are qualitative and lack the resolution required for use in prioritizing alien species in terms of pest potential (Smallwood and Salmon, 1992).

More recently, Scott and Panetta (1993) developed a method of predicting weed status for southern African plants introduced to Australia. Statistical techniques (multiple logistic regressions) revealed that problem species are typically widespread, "weedy", are found in a range of climates in southern Africa, and have been established in Australia for a long time (longer than 140 years for the best fitting regressions). For agricultural weeds, existence of congeneric weeds in southern Africa and climatic range (taken together), and the single variable "weed status in southern Africa", were found to be good predictors of weed status in Australia. It was significant that no suitable predictors of weed status were found for non-agricultural (environmental) weeds.

Smallwood and Salmon (1992), using alien bird and mammal pests with well known invasion histories, developed a rating system to prioritize research and control of established problem alien organisms. They used four additive criteria: potential to be introduced, to establish, to cause damage and to be controlled. Their concern is broader than the screening of intentionally introduced species, extending to accidental introductions and prioritization of candidate species. Furthermore, the authors claim that the approach is easily adapted for use anywhere. Modifications would centre around "location-specific concerns for natural areas, resources, agricultural production systems, and human health" (Smallwood and Salmon, 1992)—i.e. human concerns rather than characteristics of organisms and receiving environments.

Our expert system focuses on specific interactions between the fynbos environment and characteristics of species likely to be introduced. Although the questions and rules may be applicable to some extent to other mediterranean-type shrublands, we make no claims of generality of the system. Barriers and windows to invasion are different in different environments. The *approach* described here—a *simple* expert system providing practical "rules of thumb" derived from empirical evidence and pertaining to the biology of the organisms involved and characteristics of the receiving environment—can certainly be applied elsewhere. The level of information required for a rigorous assessment is perhaps best shown by the level of detail required for assessment of *Banksia* taxa in section 4.4. The prerequisite is therefore considerable insight into the relevant ecological interactions and processes. The other two approaches require no understanding of the mechanisms of the invasion process. For this reason, they are more general. Scott and Panetta (1993) are aware of this problem in their "sociological" approach and suggest that it may account for their finding relationships for agricultural weeds and not for environmental weeds; agricultural weeds are more closely associated with human activities.

Ranking of species within the categories of high- and low risk was not an objective of this study. However, we suggest the following order of invasive potential for the classifications: LR1i<LR1ii<LR1iii<. . .<LR5<HR3<HR2<HR1. Differential invasive success within genera, or species exploiting similar invasion windows, due to differences in reproductive output, for example, could add to the resolution within the class LR4. The relationship is complicated by the fact that for many species, more than one barrier may apply. Untangling the complexities of combinations of strategies renders the problem of ranking intractable. For practical purposes, the two categories "low risk" and "high risk" will probably suffice.

The length of time since introduction is clearly an important factor in invasions and in predicting weed status (e.g. Scott and Panetta, 1993). One interpretation of this observation is that invasion windows may "open" only under exceptional conditions, e.g. as a result of an unusually long dry season or short fire interval facilitating establishment. Once established, the species might generate very large numbers of persistent seeds enabling it to continue to proliferate in conditions where it was previously unable to establish. Crawley (1989) discusses the interaction of chance events and timing in determining community structures. Noble and Slatyer (1980) give further examples illustrating dramatic differences in resulting community structure depending on the timing of an event. The longer an alien organism resides in an area (in cultivation for example), the more likely it will encounter conditions suitable for establishment (outside of cultivation). Therefore, use of mean and expected values for attributes of the receiving environment and species attributes are not sufficient for predicting invasive success. Maxima and minima (e.g. minimum fire return time, maximum seed bank longevity, etc.) may be of more significance when heuristically combined with experience of the invasion process (cf. Ralls and Starfield, 1995).

4.6. ADVANTAGES OF THE EXPERT SYSTEMS APPROACH

The logic behind the system can be conceptualized as a decision tree (see flow diagrams in Figures 1–7). Decision trees provide a straightforward method of reaching a decision, but the flow charts tend to be too cryptic and awkward when referring to supplementary notes for more complete explanations of the requirements of particular questions. Where necessary, the expert system provides as much as a full screen of supportive information, and more if required.

The usual benefits of expert systems also apply. A formalized and automated inference mechanism underlies the reasoning, eliminating human error in this facet. One of the most important advantages of the system is its *transparency*. Its reasoning is easily followed both during the session (through the help facilities), and after a species has been classified (through the *explain* feature). The *explain* feature provides a detailed explanation for the system's classification and the user may justify a final decision by accepting or rejecting the system's conclusions at any point in the path to a decision. Expert systems excel in situations where reasoning with incomplete or uncertain data is necessary. This is almost always the case in ecology where true replication does not occur, data sets are never complete, but decisions have to be made nevertheless. The expert system described here does not explicitly deal with uncertainty. Confidence in the system's conclusions is set by the extent to which users accept the underlying assumptions of the rules.

Crawley (1987) argued that: "We may never be able to predict which of a set of invaders is likely to establish, and which, having become established, is likely to become the most abundant" (see Richardson and Cowling, 1992, for further discussion on this pessimistic view). We are fully aware of the idiosyncracies of invasions, but suggest that it is indeed feasible to gain predictive understanding *for particular systems* if the "mechanics" of the invasion process are adequately understood. If one can identify the barriers that need to be overcome, and then examine the attributes of species of interest, then one can go a long way towards assessing the risk of invasion by that species in the particular environment. At the very least, species with low invasive risk can be identified.

4.7. IMMEDIATE USES

In the absence of strict legislation and control on the importation of alien plants (cf. Glavovic, 1993), the system was developed to make the point that some form of prediction is possible, and that risk assessment may be achieved relatively simply for improved decision-making. The system can be used to assess the invasive risk associated with the introduction of particular woody trees and shrubs—species which fall into Swarbrick's (1991) "canopy dominant weeds" category. If one intends to introduce a species for commercial reasons and does not have all the information the system requires, a high risk classification may well result. By recording unknown responses the user can then identify the specific information that must be obtained or areas for research. The system also has potential for modelling and other types of scenario testing by experimenting with the fynbos defaults set at the start of a session. For example, the system may be used by managers to investigate the risk status of particular species with respect to different fire management strategies. The defaults may also be manipulated in terms of altered rainfall and fire cycles predicted by models of global warming. The risk status of many introduced species is likely to change.

Another potential application is for teaching the concepts of biological invasions. Developing an expert system is a useful educational exercise in itself. The principle benefit is in learning to synthesize information (Starfield and Bleloch, 1991). Reasoning is necessarily explicit and consistent. Both inferential and factual knowledge are accessible. Furthermore, experimenting with the finished expert system and exploring the information contained in help screens and *hypertext* attachments can also be very informative. The system has proved very useful for training Conservation Biology students at the M.Sc. level.

4.8. FUTURE DEVELOPMENTS

The system could be expanded to categorize the species to be introduced according to Swarbrick's (1991) scheme; species could then be screened accordingly. At present, more than 50% of the conservation budget for mountain catchments in the southwestern Cape is allocated to combatting alien plants (Richardson and Cowling, 1993). Most of this is used for control of the most serious invaders which are all "canopy dominant weeds" *sensu* Swarbrick (1991). It may be some time before due attention can be paid to invaders with less obvious impacts.

In view of the limited user-base at present, the user interface and help facilities (including a *hypertext* attachment for background information) have not been fully developed and evaluated. These aspects could be very useful as the user base extends to a broader range of horticulturalists and nature conservancies. In the current version, the system is clearly very responsive at each level. It simply outputs a result and exits if low risk is indicated, or proceeds to an independent module. Future versions will require comprehensive sensitivity analyses and tests of robustness.

The underlying knowledge of this system may become an integral part of an expert system for prioritizing and designing control strategies for established invaders. Control measures can be directed towards critical stages in the invasion process. For example, if reproductive output is very high, seed-attacking biocontrol agents should be considered. The existence of a suitable specialist seed predator could reduce the level of risk associated with a species. As a decision support tool in this context, the system may be supplemented with *hypertext* and modelling components for ready access to relevant background information. The modelling component could consist of simple individual-based models (cf. DeAngelis and Gross, 1992) using cellular automata (see McGlade, 1993, for background information, and Colasanti and Grime, 1993, for a relevant example) to graphically illustrate relative rates of alien spread given various parameters (e.g. juvenile period, number of seeds produced, seed-wing loading, prevailing wind velocity etc.).

5. Conclusions

The expert system approach shows great promise in the area of decision support for the screening of potentially invasive plants in fynbos. The development cycle can yield valuable insights into specific mechanisms of invasion and the finished product comprises a defendable component of the decision process. An expert system can draw attention to the factors to be considered when assessing the invasive risk of a species and indicate areas for further investigation/research.

In contrast to the more standard statistical or "sociological" approaches (e.g. Scott and Panetta, 1993), this approach is close to the biology of the specific classes of organisms involved and their likely interactions with the target environment. This is a move away from generalized mathematical models, predicting average or expected behaviours, towards the level of specific ecological interactions. When developing heuristics for this type of risk assessment, the extremes, rather than average behaviours, are often of more significance. The system is designed to enable anyone who intends to introduce a woody tree or shrub into the fynbos biome for cultivation to screen the plant and indicate why the species is not likely to invade, if that is indeed the case; otherwise a high risk classification will result. Provided the heuristics are approved by conservationists, this procedure should be mandatory, in advance of any introductions, at the introducer's expense. Shifting the responsibility onto developers obviates the need for conservationists to identify open ended sets of "noxious weeds".

The expert systems approach does not aspire towards a generalized theory of the invasion process. The aim is to produce a set of practical heuristics for better, defendable real-world decisions, in the absence of valid theory and complete data.

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A run-time version of the system is available (without support) from the Institute of Plant Conservation, University of Cape Town, at a cost of US$15 to cover handling costs, the disk and postage.

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Appendix 1

Questions and associated rationale for assessment of the risk of invasive success of introduced plants in fynbos.

1. Is intense fire a prominent characteristic of the home environment and does the area have a fire-adapted biota? **(yes/no)**. It is assumed that only species from fire-prone systems will invade fynbos (Rule 18).
2. What is the typical fire return time (in years) in the home environment (enter 40 if unknown)? **(enter a number between 0 and 40)**.
3. With respect to total N and P in the soil, is the home environment nutrient-poor? **(yes/no/unknown)**. Nutrient-poor soils are those with total soil nitrogen and phosphorus contents of <0·3% and <0·06%, respectively. These values characterize the soils of mediterranean-type ecosystems in Australia, California and the Mediterranean Basin (the source of all the invasive taxa listed in Table 1).
4. What is the annual rainfall in the home environment (mm)? **(enter a number)**. It is assumed that a species will not invade unless the annual rainfall in the home environment is at least as much as the minimum annual rainfall in fynbos (Rule 1). The default value is 400 mm. No species from areas with lower rainfall have invaded fynbos.
5. In what type of vegetation does the species occur in its home range? **(mediterranean-type shrubland, dry forest, wet forest, savanna)**. Only species occurring in mediterranean-type shrubland or dry forest are deemed worthy of further investigation. No wet forest and savanna species have been known to invade fynbos.
6. In its home environment the species typically occurs as ______? **(isolated individuals/isolated individuals but occasionally thicket-forming or "weedy"/a thicket-forming or "weedy" species)**. Habitat specific species which occur as isolated individuals in a habitat restricted in fynbos are dismissed as low risk (Rule 9).
7. In its home environment, is the species obviously a habitat specialist? **(yes/no)**. For example, is it restricted to riparian zones or to a particular soil type with restricted distribution. The habitat restriction may be abiotically (e.g. soil nutrient characteristics) or biotically determined. If biotically determined, equivalent biotic agents must be present in fynbos for successful invasion.
8. The species has been identified as a habitat specialist. Is this habitat specialization biotically determined? **(yes/no/unknown)**.
9. Is it likely that any biotic agents will have the same effect in fynbos? **(yes/no)**.
10. Is this habitat restricted in fynbos? **(yes/no)**.

    The ability to disperse over fairly "long" (see Question 14) distances adds to the invasive risk associated with a species. In general, species whose seeds are dispersed by water, invertebrate animals (e.g. ants) or gravity do not invade fynbos. Species whose seeds are dispersed over long distances by vertebrate animals (e.g. birds) and wind, however, stand a better chance of invading. In the case of vertebrate animals, the system asks whether the dispersal agent is a generalist or specialist (in the home environment). If specialist, and there is no equivalent in fynbos, the species is classified as low risk (Rule 11). Otherwise the system continues with questions concerning seed production (Question 15).
11. What is the principle dispersal vector? **(water/invertebrate animal(s)/gravity/**

vertebrate animal(s)/wind). If the species exhibits more than one mode of dispersal, select the one which disperses furthest. For example, *Acacia longifolia* is dispersed by ants and birds, but vertebrate animals (birds) disperse seeds further than do ants, and are more important for widespread invasion.

12. The seeds are dispersed by vertebrate animals. Does the species require a specialist dispersal vector? **(specialist/generalist).**
13. Is there an equivalent dispersal vector in fynbos? **(yes/no).**
14. Does the seed have adaptations, such as a low seed-wing loading, for dispersal over long distances by wind? **(yes/no).** "Long distance" means that dispersal over several hundred metres is common. Short distance means that seeds are seldom dispersed further than 100 metres.

A species may be dismissed as low risk if its cumulative seed production between fires is low. Even if low in the home environment, the system investigates the effects of biotic determinants of reproductive output. If a biotic determinant of reproductive output has a positive effect in the home environment and is not present in fynbos (and there is no analogue), the species is classified as low risk (Rule 14). If a biotic determinant of reproductive output has a negative effect in the home environment and the organism (or an analogue) is present in fynbos, the species is dismissed as low risk. Otherwise, seed production is assumed to be high and seed predation is considered which, if high, may reduce the risk of invasion associated with the species.

15. In its home environment, the annual seed production (number of plump seeds produced per plant) is ______? **(low/medium/high)** (0–50, 50–500, >500 respectively; see Richardson *et al.*, 1990 for discussion). For serotinous plants or any species with a seed bank (in the canopy or soil) this refers to the *cumulative* seed production, i.e. the seed bank at the average fire return interval for the target environment (12 years for fynbos).
16. The determinant of reproductive output is ______? **(biotic/genetic/unknown)**
17. Does the biotic determinant of reproductive output have a positive effect? **(yes/no).**
18. Seed production is low, reproductive output is biotically determined. Is the determinant of reproductive output present in fynbos? **(yes/no).**
19. Is there an equivalent determinant of reproductive output in fynbos? **(yes/no).** It is assumed that equivalent (or the same) biotic agents in fynbos will have the same effect as they do in the home environment. Crawley (1987) describes an example which throws doubt on this assumption: the gall forming cynipid wasp, *Andricus quercuscalicis*, and *Quercus robur* in the U.K.

If seed predation is likely to be high in fynbos (relative to the home environment) and if seed predation in the home environment is largely by generalists, the species is classified as low risk (Rule 16). Otherwise, life history adaptations to the type of fires characteristic of fynbos are considered as the final filter (Questions 22–24).

20. Pre- and post-dispersal seed predation. Relative to the home environment, seed predation in fynbos is likely to be ______? **(higher/lower/the same/unknown).** For example, if the species has special seed protection structures such as follicles that exclude all but specialized seed predators (that are not introduced simultaneously) then pre-dispersal seed predation in fynbos will probably be low.
21. Is the seed predator a specialist? **(yes/no/unknown)** i.e. in the home environment is the majority of the net seed loss (pre- and post-dispersal) attributable to

biotic agents caused by specialist animals, or by a range of generalists?
The highest risk is posed by species which have not been excluded on any of the preceding criteria and are capable of producing viable seeds within a single fynbos fire cycle (Rule 3). Species with longer juvenile periods but able to withstand the intense fires characteristic of fynbos constitute the next highest risk category (Rule 4). The final high risk category is for species with a longer juvenile period than the typical fynbos fire interval, a poor fire survival capacity but whose seed banks persist for longer than the typical fire return time in fynbos (Rule 5).

22. The juvenile period of the species is ______ years **(enter number)**. At what age is mature seed available for re-establishment, or how long after fire/germination does the species produce viable seed (minimum time)?
23. The fire survival capacity of adult plants is ______? **(good/poor)**.
24. The seed bank longevity is ______ (in years)? **(enter number)**. How long do seeds in the seed bank remain viable?

Appendix 2

Rules for the allocation of risk status to introduced plants in fynbos.

1. IF
Fynbos_Min_Annual_Rainfall<Home_Environment_Annual_Rainfall
THEN
Annual_Rainfall_Similar {i.e. fynbos rainfall acceptable}

2. IF
NOT LR AND {not low risk}
(HR1 OR HR2 OR HR3) {high risk 1, 2 or 3}
THEN
HR {high risk}

3. IF
NOT LR AND {not low risk}
Juvenile_Period_Short=1 {true}
THEN
HR1 {high risk 1}

4. IF
NOT LR AND
Juvenile_Period_Short=0 AND {long juvenile period}
Fire_Survival_Capacity=1 {good fire survival capacity}
THEN
HR2 {high risk 2}

5. IF
NOT LR AND {not low risk}
Juvenile_Period_Short<0·5 AND {long juvenile period}
Fire_Survival_Capacity=0 AND {poor fire survival capacity}
Seed_Bank_Longevity>0·5 {long lived seed bank}
THEN
HR3 {high risk 3}

6. IF
Fynbos_Typical_Fire_Return_Time>Juvenile_Period
THEN
Juvenile_Period_Short

7. IF
LRi OR LRii OR LRiii OR LRiv OR LR1 OR LR2 OR LR2b OR
LR3 OR LR4 OR LR4a OR LR4b OR LR5
THEN
LR {low risk}

8. IF
Home_Environment>1 {not mediterranean-type shrubland or dry forest}
THEN
LR1 {low risk 1—home environment risk}

9. IF
NOT LR1 AND {not low risk}
Population_Characteristics = 0 AND {isolated individuals}
Habitat_Specialist = 0 AND {yes/true}
(Habitat_Specialisation_Biotically_Determined = 0 OR {no}
Habitat_Specialisation_Biotically_Determined = 1 AND {yes}
Equivalent_Biotic_Agents_in_Fynbos = 0) AND {yes}
Habitat_Restricted_in_Fynbos = 0 OR {yes}
LR2b {rule 10}
THEN
LR2 {low risk—habitat specialisation}

10. IF
Population_Characteristics = 0 AND {isolated individuals}
Habitat_Specialist = 0 AND {yes}
Habitat_Specialisation_Biotically_Determined = 1 AND {yes}
Equivalent_Biotic_Agents_in_Fynbos = 1 {no}
THEN
LR2b {due to biotically determined habitat specialisation, risk is low}

11. IF
NOT LR2 AND {rule 9}
Principle_Dispersal_Vector = 3 AND {vertebrate animals}
Dispersal_Vector_Specificity = 0 AND {specialist}
Equivalent_Dispersal_Vector_in_Fynbos = 0 OR {no}
LR3a OR {see rule 12}
LR3b {see rule 13}
THEN
LR3 (dispersal risk is low)

12. IF
NOT LR2 AND {rule 9}
Principle_Dispersal_Vector = 0, 1 or 2 {water/invertebrate animals/gravity}
THEN
LR3a {low risk}

13. IF
NOT LR2 AND {rule 9}
Principle_Dispersal_Vector = 4 AND {wind}
Inherent_Seed_Dispersability = 0 {short}
THEN
LR3b {low risk}

14. IF
NOT LR3 AND {rule 11}
Annual_Seed_Production = 0 AND {low}
Determinant_of_Reproductive_Output = 0 OR {genetic}
Annual_Seed_Production = 0 AND {low}
Determinant_of_Reproductive_Output = 1 AND {biotic}
Positive_Effect = 0 AND {yes—positive effect}
Organism_Present_in_Fynbos = 0 AND {no}
Equivalent_Determinant_of_Reproductive_Output = 1 {no}
THEN
LR4 {genetic reproductive output risk is low}

15. IF
NOT LR4 AND {rule 14}
Annual_Seed_Production = 0 AND {low}
Determinant_of_Reproductive_Output = 1 AND {biotic}
Positive_Effect = 1 AND {no—negative effect}
(Organism_Present_in_Fynbos = 1 OR {yes}
Organism_Present_in_Fynbos = 0 AND {no}
Equivalent_Determinant_of_Reproductive_Output = 0) {yes}
THEN
LR4a {biotic reproductive output risk is low}

16. IF
NOT LR4a AND {rule 15}
Seed_Predation = 0 AND {high}
Specialist_Predator = 0 {yes (in home environment)}
THEN
LR4b {risk, reduced by seed predation, is low}

17. IF
NOT LR4b AND {rule 16}
Juvenile_Period_Short<0·5 AND {no, long}
Fire_Survival_Capacity = 0 AND {poor}
Seed_Bank_Longevity_Long<0·5 {short}
THEN
LR5 {juvenile period long, fire survival poor, seedbank short-lived—risk low}

18. IF
Fire_Characteristic_of_Home_Environment = 0 {no}
THEN
LRi {intense fires are not prominent in the home environment: low risk}

19. IF
Similar_Fires<0·5 {not similar}
THEN
LRii {risk due to fire similarity is low}

20. IF
Similar_Nutrients=0 {not similar}
THEN
LRiii {risk, due to dissimilar soil nutrient characteristics, is low}

21. IF
NOT Annual_Rainfall_Similar
THEN
LRiv {risk, due to dissimilar rainfall is low}

22. IF
Seed_Bank_Longevity>Fynbos_Min_Fire_Return_Time
THEN
Seed_Bank_Longevity_Long

23. IF
Fire_Characteristic_of_Home_Environment AND
Home_Environment_Fire_Return_Time>Fynbos_Min_Fire_Return_Time
THEN
Similar_Fires