Introduction

The several objectives of this book can be stated in the form of simple questions. What can we conclude about the nature of grass seed dormancy in a single, well-studied, species? Are there commonalities between seed dormancy in this single species and other grass species? Can new conclusions be reached about the nature of the physiological and environmental conditions that establish the state of dormancy in grass seeds? Is it possible to describe new models for seed dormancy that simplify our understanding of grass seed dormancy?

The nature of the first question is in part a semantic problem related to correctly matching the etymological meaning of a word to the reality it attempts to describe. The English word 'dormancy', derived from the French *dormir* (to sleep), itself derived from the Latin *dormire* (to sleep), is defined in the *Concise Oxford Dictionary* as 'lying inactive in sleep'. However, biologists have found that this definition does not encompass observed seed behaviour. Hence the many attempts to divide dormancy into sub-categories that cover the situations in nature where some seeds fail to germinate, whereas others can, in a specific environment (Amen, 1968; Bewley & Black, 1982; Lang *et al.*, 1987).

An adequate description of dormancy must involve at least three major components viz. the seed, the environment and a time element describing changes in state of both the seed and environment. In addition, it is useful to have some measure of incidence of dormancy related to genetic variation in a plant population. The definition of dormancy should be applicable to an individual seed or to groupings up to the population level.

Some years ago I drew attention to the fact that most of the published experimental approaches to understanding the nature of dormancy, as a general phenomenon in biology, have been based on the reductionist approach (Simpson, 1978). This approach emphasises the systematic division of the organism into its constituent parts down through successively lower levels of organisation to the current limits of biological, biophysical and biochemical technology. Using this approach, analysis down to the level of constituent molecules is expected to 'explain' seed dormancy. For example, molecules that inhibit, or promote, germination have been invoked as the *raison d'étre* for the presence or absence of dormancy. However, modern systems analysis applied to biology (Koestler, 1967; von Bertalanffy, 1968; Whyte *et al.*, 1969) stresses that the dormancy system includes both the organism and its environment within some specified time period. The whole system is organised into hierarchies of functional and structural levels that are difficult to separate. In a systems description of function the requirements on one level of action are also the constraints on the next level. Thus normal activity at one functional level can only take place when all levels below that level are functioning properly. A functional description of seed dormancy may involve a few or many different levels in the hierarchy depending upon the interest of the observer. A useful description of dormancy may be found in the holistic general view of the system or alternatively at a very detailed sub-level.

The first three chapters show the extent of seed dormancy in the grass family and systematically outline the structural factors within the plant, and the environmental factors encompassing the plant or seed dispersal unit, that together comprise the seed–environment system. Chapters 4 and 5 describe the physiological nature of dormancy, seen through a systems perspective, as well as several approaches to modelling a dormant seed system. A conclusion is reached that there is no single state of seed dormancy common to all grass species. There are as many states of dormancy as there are species, and within species the potential number of states of dormancy increases in direct proportion to the intensity with which observations are carried out on seeds to the lowest levels of the seed–environment system. The view of 'reality' about the state of seed dormancy, or germination, is related as much to the view adopted by the observer as it is to the degree of internal constraint and patterns of determinate behaviour originating from the living system we call a seed.

1

The occurrence of dormancy in the Gramineae

'The grass family is one of the largest and most diverse in the plant kingdom and certainly one of the most important. More than any other, this assemblage of plants feeds man and beast and so clothes the earth that soil may be built and held securely from the forces of erosion. No other group of plants is more essential to the nutrition, well being, or even existence of man.'

J. R. Harlan, 1956
(Theory and Dynamics of Grassland Agriculture)

Gould (1968) has divided the family of grasses (Gramineae) into 25 tribes and 177 important genera. Seed dormancy occurs within 18 of the tribes and has been recorded in one or more species in at least 78 of the genera (Table 1.1). Seed dormancy is one of a number of adaptive traits, such as seed size and shape, that are polymorphic in character. Together these characteristics provide diversity and fitness for both opportunistic settlement and enduring occupation of temporally and spatially diverse habitats (Jain & Marshall, 1967). Within each grass species there can be considerable variation in the degree of polymorphism associated with the expression of seed dormancy. The degree of polymorphism is a function of the form of reproduction (self- or cross-pollination) in each species. Some species rely on genetic diversity and others on phenotypic plasticity for adapting to varying environments through the trait of seed dormancy. Dormancy has been described as an adaptive trait that causes seeds to germinate at a time, or place, favourable to the subsequent survival of the seedling and adult plant (Pelton, 1956).

The grass family occurs in a great diversity of form spread over a wide range of habitats. Grasses survive in even the most stressful extremes of climate (Simpson, 1981) and show great evolutionary plasticity (Harlan, 1956). This plasticity is due to the wide variety of modes of reproduction with aneuploidy and polyploidy. The most common form of reproduction is by cross-fertilization from wind-borne pollen. Nevertheless all methods of fertilization from enforced cross-pollination all the way to obligate self-fertilization, and intermediates, exist among grass species. Because seed dormancy is known to be a genetically inherited trait (Naylor, 1983)

Table 1.1. *List of tribes and genera of the Gramineae (After Gould, 1968) indicating:*
(a) Number of publications about seed dormancy for the genus retrieved in a computer search of world literature – an index of incidence of seed dormancy.
(b) Number of species in the genus listed as weeds (After Holm et al.*, 1979)*
(c) Geographical distribution of species estimated by average number of countries in which each species is considered a weed problem (After Holm et al.*, 1979).*

SUBFAMILY I FESTUCOIDEAE

Tribe 1. Festuceae – Bromus (37, 26, 5), Brachypodium (1, 1, 1), Vulpiea (4, 6, 3), Festuca (28, 6, 3), Lolium (37, 9, 12), Leucopoa (–, –, –), Scolochloa (1, –, –), Sclerochloa (–, 1, 1), Catapodium (–, –, –), Puccinellia (1, 4, 1), Poa (77, 7, 15), Briza (–, 3, 10), Phippsia (–, –, –), Coleanthus (–, –, –), Dactylis (20, 2, 20), Cynosurus (3, 2, 7), Lamarckia (–, 1, 7).

Tribe 2. Aveneae – Koeleria (1, 1, 8), Sphenophlis (–, –, –), Trisetum (1, 1, 1), Coryenphorous (–, –, –), Aira (5, 3, 2), Deschampsia (4, 3, 4), Scribneria (–, –, –), Avena (931, 11, 10), Ventanata (–, –, –), Helictotrichon (–, –, –), Arrhenatherum (3, 3, 4), Holcus (2, 4, 4), Dissanthelium (–, –, –), Calamagrostis (2, 5, 1), Ammophila (–, 2, 2), Apera (2, 1, 12), Polypogon (1, 3, 7), Mibora (–, –, –), Cinna (–, –, –), Limondea (–, –, –), Anthoxanthum (2, 2, 6), Hierochloe (–, –, –), Phalaris (18, 9, 13), Alopecurus (10, 12, 7), Phleum (17, 3, 4), Gastridium (–, 1, 6), Lagurus (–, 1, 5), Milium (–, –, –),Beckmannia (–, 1, 1), Agrostis (17, 14, 3).

Tribe 3. Triticeae – Elymus (1, 2, 2), Sitanion (–, –, –), Taeniatherum (–, 1, 1), Hystrix (–, –, –), Hordeum (215, 13, 5), Agropyron (33, 6, 7), Triticum [including Aegilops] (190, 8, 1), Secale (14, 2, 5).

Tribe 4. Meliceae – Melica (–, –, –), Glyceria (1, 3, 3), Catabrosa (–, –, –), Pleuropogon (–, –, –), Schizachne (–, 3, 1).

Tribe 5. Stipeae – Stipa (22, 10, 2), Oryzopsis (29, 2, 4), Piptochaetium (–, –, –).

Tribe 6. Brachyelytreae – Brachyelytrum (–, –, –).

Tribe 7. Diarrheneae – Diarrhena (–, –, –).

Tribe 8. Nardeae – Nardus (1, 1, 3).

Tribe 9. Nonermeae – Nonerma (–, –, –), Parapholis (–, 1, 5).

SUBFAMILY II. PANICOIDEAE

Tribe 10. Paniceae – Digitaria (25, 32, 8), Leptoloma (–, 8, 8), Anthaenantia (–, –, –), Stenotaphrum (–, 3, 3), Brachiaria (10, 19, 7), Axonopus (1, 4, 10), Reimarochloa (–, –, –), Eriochloa (–, 6, 3), Paspalum (14, 37, 7), Paspalidium (–, 3, 4), Panicum (57, 82, 3), Lasiacis (–, 2, 2), Oplismenus (–, 6, 3), Echinochloa (36, 15, 13), Sacciolepis (–, 7, 3), Rhynchelytrum (–, 2, 19), Setaria (38, 26, 10), Pennisetum (19, 14, 7), Cenchrus (5, 15, 5), Amphicarpum (–, 1, 1), Melinus (–, 1, 8), Anthophora (–, –, –).

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Table 1.1. *(cont).*

SUBFAMILY I FESTUCOIDEAE

Tribe 11. Andropogoneae – Imperata (2, 5, 12), Miscanthus (1, 5, 2), Saccharum (12, 5, 7), Erianthus (–, –, –), Sorghum (42, 12, 8), Sorghastrum (7, –, –), Andropogon (13, 27, 3), Arthraxon (–, 1, 4), Mirostegium (–, –, –), Dichanthium (1, 3, 5), Bothriochloa (7, 5, 1), Chrysopogon (1, 3, 7), Hyparrhenia (–, 4, 6), Schizachyrium (13, 3, 1), Eremochloa (1, 1, 1), Trachypogon (–, –, –), Elyonurus (–, –, –), Heteropogon (1, 1, 11), Manisuris (–, –, –), Hackelochloa (–, 1, 7), Tripsacum (–, 1, 5), Zea (23, –, –), Coix (–, 5, 8).

SUBFAMILY III. ERAGROSTOIDEAE

Tribe 12. Eragrosteae – Eragrostis (27, 51, 5), Neeragrostis (–, –, –), Tridens (–, –, –), Triplasis (1, –, –), Erioneuron (–, –, –), Munroa (–, –, –), Vaseyochloa (–, –, –), Redfieldia (–, –, –), Scleropogon (–, 1, 3), Blepharidachne (–, –, –), Calamovilfa (–, 5, 1), Lycurus (1, –, –), Muhlenbergia (2, 5, 1), Sporobolus (4, 18, 4), Blepharoneuron (–, –, –), Crypsis (–, 2, 2).

Tribe 13. Chlorideae – Eleusine (17, 6, 13), Dactyloctenium (2, 2, 27), Leptochloa (–, 8, 8), Trichoneura (–, 2, 5), Gymnopogon (–, –, –), Tripogon (–, –, –), Willkommia (–, –, –), Schedonnardus (–, 1, 1), Cynodon (13, 1, 85), Microchloa (–, –, –), Chloris (12, 14, 6), Trichloris (–, 3, 6), Bouteloua (11, 3, 1), Buchloe (4, 1, 1), Cathestecum (–, –, –), Aegopogon (–, –, –), Tragus (–, 3, 3), Spartina (1, 5, 1), Ctenium (–, –, –), Hilaria (1, –, –).

Tribe 14. Zoysieae – Zoysia (7, 4, 4).

Tribe 15. Aeluropodeae – Distichlis (1, 3, 3), Allolepis (–, –, –), Monanthochloe (–, –, –), Swallenia (–, –, –).

Tribe 16. Unioleae – Uniola (2, –, –).

Tribe 17. Pappophoreae – Pappophorum (–, –, –), Enneapogon (–, –, –), Cottea (–, –, –).

Tribe 18. Orcuttieae – Orcuttia (–, –, –), Neostapfia (–, –, –).

Tribe 19. Aristideae – Aristida (11, 15, 2).

SUBFAMILY IV. BAMBUSOIDEAE

Tribe 20. Bambuseae – Arundinaria (1, 1, 1).

Tribe 21. Phareae – Pharus (–, –, –).

SUBFAMILY V. ORYZOIDEAE

Tribe 22. Oryzeae – Oryza (162, 8, 1), Leersia (1, 3, 11), Zizania (21, 1, 1), Zizaniopsis (–, 2, 2), Luziola (–, 1, 1), Hydrochloa (–, 1, 1).

SUBFAMILY VI. ARUNDINOIDEAE

Tribe 23. Arundineae – Arundo (–, 3, 5), Phragmites (1, 5, 17), Cortaderia (–, –, –), Molinia (–, –, –).

Tribe 24. Danthonieae – Danthonia (5, 1, 1), Sieglingia (–, –, –), Schismus (–, 1, 1).

Tribe 25. Centotheceae – Chasmanthium (–, –, –).

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diversity in the mechanisms for achieving seed dormancy can be expected in the grass family because of the diversity in methods of reproduction. One of the major objectives of this book is to determine whether there are just a few, or many, ways of achieving seed dormancy in the grass family.

The grass family can be arbitrarily divided into several categories that reflect their utilitarian value for human needs. Sub-division into wild, forage, cereal and weed grasses in contrast to the taxonomic divisions also gives some indication of the diversity of geographical and agronomic situations in which members of the grass family perform valuable functions.

Seed dormancy has a natural significance for survival of grasses in their undisturbed ecosystem. In addition seed dormancy creates a number of difficulties in the systems of animal and crop husbandry that supply a high proportion of the human diet. Animal husbandry is based on the utilization of both natural grasslands and sown pastures of improved forage grasses. Seed dormancy can be a major problem in the establishment of grasses used for pastures. Crop husbandry based primarily on annual cereal grasses depends on uniform germination hence seed dormancy can cause serious problems at the time of establishment of the crop. Seed dormancy, combined with high seed production, is a primary cause of the persistence of many grass species as weeds competing effectively in the major crops of the globe. Many grasses also have a nuisance value in non-crop localities such as lakes, canals, road sides, railway tracks, airfields and public parks. In these areas of increasing importance linked to the urbanization of a rapidly growing human population seed dormancy plays an important role in the survival of plant species. In recent years the concern for preservation of the genetic diversity of both wild and cultivated plants through the use of gene banks has drawn attention to the difficulty of germinating seeds of many grass species because of persistent seed dormancy (Ellis, Hong & Roberts, 1985b).

In the following sections of Chapter 1 the above somewhat arbitrary categories of wild, forage, cereal, and weed grasses will be assessed for the occurrence and level of significance of seed dormancy occurring in natural and manipulated ecosystems.

1.1 Wild grasses

The term 'wild' is used as a general category for all those species that have not been deliberately modified through selection pressure and breeding methods applied by mankind. 'Wild' grasses comprise the majority of grass species. Even if the top 250 global weeds and the major global crops (about 50 species (Stoskopf, 1985)) were all grasses and these were then added to the total of about 44 cultivated pasture grasses the grand total would be a tiny fraction of the approximately 10 000 species of the family Gramineae (Semple, 1970).

It has been pointed out a long time ago (Bews, 1929) that for the majority of grasses there is no economic interest. Thus useful information, other than the simplest morphological description necessary to define taxonomic position, is absent for a majority of grass species. For this reason alone it is difficult to assess the occurrence of dormancy in the 'wild' species. Many of the species found today may represent intermediate stages between the fossil grasses of the bamboo or bamboo-like plants that existed in the Cretaceous period (Semple, 1970) and more modern genera. Seed dormancy is found in bamboos (McClure, 1966; Matumura & Nakajima, 1981) and some species such as *Melocanna baccifera* exhibit vivipary (McClure, 1966). This suggests, in an evolutionary sense, that seed dormancy and vivipary have been important traits in the grass family for a very long period of time.

1.2 Forage grasses

Cultivated forage grasses are mainly selections, starting about the middle of the nineteenth century, of native and introduced grasses with superior productivity. Forage grasses have not yet been substantially altered by plant breeding so that their characteristics are in the main similar to their wild forms. Unlike natural grasslands, modern arable pasture systems need to be frequently re-established as part of a rotational cropping system. Thus seed dormancy in forage grasses prevents successful establishment of a new pasture. Seed dormancy in one of a mixture of grass species can lead to the complete elimination of the species during the establishment phase.

Many native grasses and grassy weeds are utilized as forages and the distinctions between a cultivated forage, a weedy grass, and a native grass disappear in some regions of severe drought when all plants are severely over-grazed. This is particularly true where nomadism still prevails.

Seed dormancy is evidently very common in species belonging to the major grass genera utilized for grazing around the world (Table 1.2). Grasses from the tropical, sub-tropical, and temperate climates can all show seed dormancy. Within genera it is common to find a number of closely related species with seed dormancy. While the sample of approxima-

Table 1.2 *Evidence from the literature of the general occurrence of seed dormancy in forage grasses. The citation is the most recent reference and the number in the column indicates the number of other earlier references in* Bibliography of seed dormancy in grasses *(Simpson, 1987). The common name is given in brackets.*

Sub-family	Tribe	Genus	Species	Reference	No.
FESTUCOIDEA	Festuceae	*Bromus* (Chess grasses)	-*japonicus* (Japanese)	Froud-Williams 1981	7
			-*diandrus*	Baskin & Baskin, 1981	–
			-*catharticus [uniloides]* Rescue grass)	Froud-Williams & Chancellor, 1986	3
			-*sterilis*	Hilton, 1987	7
			-*mollis* (Soft chess)	Ellis *et al.*, 1985b	–
			-*commutatis* (Hairy chess)	Froud-Williams & Chancellor, 1986	–
			-*inermis* (Smooth brome)	Nielsen *et al.*, 1959	3
			-*secalinus* (Chess brome)	Steinbauer & Grigsby, 1957	1
			-*tectorum* (Downy brome)	Milby & Johnson, 1987	3
		Festuca (Fescues)		Williams, 1983a	9
			-*rubra* (Creeping red)	Williams, 1983b	3
			-*arundinacea* (Tall)	Stoyanova *et al.*, 1984	6
			-*pratensis* (Meadow)	Linnington *et al.*, 1979	1
			-*ovina* (Sheep)	Nieser, 1924	–
		Lolium (Ryegrasses)		Williams, 1983b	15
			-*perenne* (Perennial)	Williams, 1983b	7

		-*multiflorum* (Italian)	Van Staden & Hendry, 1985	5
		-*rigidum* (Wimmera)	Gramshaw & Stern, 1977	3
		-*temulentum* (Darnel)	Cairns & de Villiers, 1986a	–
		-*persicum* (Persian darnel)	Banting & Gebhardt, 1979	–
	Scolochloa			
		-*festucacea*	Smith, 1972	–
	Poa	(Bluegrasses)	Naylor & Abdalla, 1982	19
		-*pratensis* (Kentucky)	Phaneendranath, 1977a	30
		-*annua* (Annual)	Sgambetti-Araujo, 1978	26
		-*trivialis* (Rough)	Froud-Williams & Ferris, 1987	7
		-*fertilis*	Kleine, 1929	–
		-*palustris* (Fowl)	Rostrup 1897/8	–
		-*compressa* (Canada)	Andersen, 1947a	9
	Dactylis		Nakamura, 1962	1
		-*glomerata* (Orchard grass, Cocksfoot)	Probert *et al.*, 1985d	17
	Cynosurus	-*cristatus* (Crested dogstail)	Schonfield & Chancellor, 1983	2
Aveneae	*Aira*	-*flexuosa*	Nelson & McLaggan, 1935	–

Table 1.2. *(cont.)*

Sub-family	Tribe	Genus	Species	Reference	No.
			-*caryophylla* (Silver hair)	Pemadasa & Lovell, 1975	–
			-*praecox*	Roberts, 1986	1
		Deschampsia	-*caespitosa* (Tufted hair)	Roberts, 1986	3
		Arrhenatherum	-*elatius* (Tall oat grass)	Roberts, 1986	2
		Holcus	-*lanatus* (Yorkshire fog)	Schonfield & Chancellor, 1983	1
		Calamagrostis	-*canadensis* (Blue joint)	Conn & Farris, 1987	1
		Anthoxanthum	-*puelli* (Sweet vernal)	Nieser, 1924	–
			-*odoratum* (Sweet vernal)	Schonfield & Chancellor, 1983	–
		Phalaris		Nakamura, 1962	1
			-*arundinacea* (Reed canary)	Berg, 1982	9
			-*minor*	Parasher & Singh, 1984	2
			-*tuberosa* (Harding grass)	Myers, 1963	3
		Alopecurus	-*aequalis* (Shortawn foxtail)	Arai & Chisaka, 1961	3
			-*myosuroides*	Froud-Williams *et al.*, 1984	4
			-*geniculatis* (Water foxtail)	Roberts, 1986	–
			-*pratensis* (Meadow foxtail)	Roberts, 1986	–
		Phleum	-*pratense* (Timothy)	Schonfield & Chancellor, 1983	13
		Agrostis (Bent grasses)		Schmidt, 1969	4