EVOLUTION OF REPRODUCTIVE SYSTEMS IN THE GRAMINEAE[1]

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ABSTRACT

From a simple hermaphrodite flower, and from a complex incompatibility system unique among the flowering plants, several breeding systems have evolved in the Gramineae. Self-compatibility is the most commonplace variant and following this mutation, habitual or facultative cleistogamy is a simple evolutionary step. Separation of the sexes to different plants as in dioecism is relatively uncommon (ca. 20 genera), and gynodioecism is much less frequent still (3–4 genera). Both are seen as escape pathways from self-compatibility; the development of such pathways is discussed. Separation of the sexes to separate flowers as in monoecism is relatively common and with the variants andromonoecism and gynomonoecism is the most substantial departure from hermaphroditism in the family. These states are also interpreted as responses to self-compatibility; and though they do not generate cross-fertilization, they assist its evolution. Pathways for the evolution of these breeding systems are described. Apomixis and the breeding system best suited are discussed.

Reproductive biology in the Gramineae begins at the transition in the shoot apex from leaf production to the initiation of inflorescence primordia and the later development of floral structures. These have been well described for numerous grasses (Barnard, 1955, 1957, 1964; Bonnett, 1966; Sharman, 1960), and are mediated by photoperiod. The review of Evans (1964) elegantly reveals data on the interplay of daylength, temperature, and vernalization on inflorescence development.

Floral induction and initiation may occur in the season of flowering (Evans, 1964), or in the season preceding inflorescence emergence (Mark, 1965; Hodgson, 1966). Inflorescence emergence is temperature or daylength dependent (Cooper, 1952; Connor, 1963; Heslop-Harrison, 1961). Temperature also controls anthesis, and later the release of pollen from anthers.

Photoperiod, however, has other effects on the reproductive cycle. It may, for example, affect the frequency of cleistogamy in facultatively cleistogamous grasses (Langer & Wilson, 1965), or in a facultative apomict the frequency of apomictic or sexual embryo sacs (Knox, 1967; Knox & Heslop-Harrison, 1966), or depress maleness (Heslop-Harrison, 1959), or reduce the number of florets in the male inflorescence of *Zea mays* (Moss & Heslop-Harrison, 1968), or control protandry and protogyny (Emerson, 1924).

Although these environmental influences are considerable, genetic influences may cause transient male and female sterility, or restore lost fertility in part or in whole, or promote redistribution of the sex-forms. A combination of both genetic and physiological factors may introduce difficulties into an interpretation of the breeding system of any grass.

At the International Symposium on Reproduction in Flowering Plants held at Christchurch, New Zealand, in 1979, I presented a survey of the breeding systems known in the Gramineae (Connor, 1980). This present paper is complementary

to that; the bibliographies of both papers supplement each other. Here, as there, I follow the organization of tribes proposed by Hubbard (1973) for the grasses.

THE FLOWER, THE SPIKELET, AND THE INFLORESCENCE

The primitive grass flower is postulated as having three bracts and lodicules, six stamens, and a 1- or 3-locular tristigmatic gynoecium (Schuster, 1910; Arber, 1934; Clifford, 1961). The spikelet is considered to have been many flowered, and the inflorescence is thought to have comprised many of these spikelets in a simple more- or less-branched, terminal panicle. Associated with these characteristics is the further postulate of entomophily (Schuster, 1910; Clifford, 1961; Stebbins, 1956, 1974).

From these very reasonable postulates there is a general evolution in the flower by reduction to two bracts and lodicules, three stamens, two stigmas and one ovule, though this combination is by no means universal. Associated features that are interpreted as part of an anemophilous syndrome are: rapidly elongating staminal filaments; easily exserted stigmata; readily dispersed pollen; a single ovule per flower; and the preservation of a self-incompatibility system.

Within the flower some further reductions are detectable, e.g., lodicules may be lacking or be so small as to be ineffective. Absence of lodicules is frequently associated with protogyny in hermaphrodite flowers but may also occur in monoecious and dioecious taxa; see summary in Connor (1980). Stamens may be reduced to two or one per flower; this state seems randomly distributed among the tribes and is independent of what seems its logical correlative—cleistogamy (Connor, 1980).

Among spikelets there are some trends in common. Geminate dimorphic spikelets of the form one sessile and the other pedicelled may be found in such different tribes as the Phareae and Olyreae (Bambusoideae) and in the Andropogoneae and Maydeae (Panicoideae). This form is frequently associated with a discrimination such that male elements alone are in pedicelled spikelets and female organs in sessile ones. A single hermaphrodite floret borne terminally in a spikelet of two or more florets may be found in the Bambuseae, Arundinelleae, Aveneae, Paniceae, and Andropogoneae. The ultimate reduction is to one floret per spikelet, and this is found in such differing tribes as Phareae, Agrostideae, and Sporoboleae.

The precise evolutionary phases displayed in inflorescence development are not topics for this paper except as they display relationships to sex-form. Among monoecious genera there is a slight trend towards axillary female inflorescences and terminal male inflorescences, e.g., *Humbertochloa*, *Hydrochloa*, *Luziola*, and *Zea*. Axillary inflorescences are a feature of some herbaceous members of the Bambusoideae; in such genera as *Arberella*, *Raddia*, and *Strephium* they occur at almost all the nodes, but in *Olyra* axillary branches occur at uppermost nodes only (Calderón & Soderstrom, 1973; Soderstrom & Calderón, 1979a). These genera are also monoecious but the axillary inflorescences are of mixed male and female spikelets.

Clayton (1969) detects in the Andropogoneae an evolution towards numerous smaller axillary inflorescences along with the development of the spathe and the

TABLE 1. Reproductive systems in the tribes of grasses; + = present.

Tribe	Hermaphro-ditism	Monoecism[a]	Dioecism[b]	Apomixis	Cleistogamy
Arundineae	+	+	+	+	
Chlorideae	+	+	+	+	+
Eragrostideae	+	+	+	+	+
Festuceae	+	+[c]	+[c]	+[c]	+
Paniceae	+	+	+	+	+
Andropogoneae	+	+		+	+
Aveneae	+	+		+	
Hordeeae	+	+		+	+
Pappophoreae	+	+	+		+

[a] Including andro- and gynomonoecism.
[b] Including gynodioecism.
[c] Mostly contributed by *Poa*.

spatheole; these form false panicles and it is supposed that they developed from an apparently primitive terminal panicle.

As a whole, most of these differences reflect morphological adaptations that were ventured upon in the grasses and have become widespread, but it is impossible to indicate what has failed to evolve or failed to succeed. This point is well developed by Clifford (1961) in discussing the possible number of symmetrical arrangements of floral organs that can be derived by reduction, and the number actually present in flowers in the family.

DIVERSITY OF REPRODUCTIVE SYSTEMS

The grasses display a wide variety of breeding systems that define their genetic architecture; these range from self-incompatible hermaphroditism through to dioecism. Hermaphrodite flowers are the most common, being absent from about 20 dioecious genera, and about 50 monoecious ones. The array of floral systems includes a marked andromonoecism and a lesser frequency of gynomonoecism; gynodioecism is rare. Heterostyly is unknown.

The extreme form of self-fertilization is seen in habitual cleistogamy, but autogamy or geitonogamy occurs in plants that flower chasmogamically, and self-compatibility is spread widely among tribes. Apomixis is recorded in about 30 genera, but apomixis, like autogamy and geitonogamy, is probably much underestimated.

An attempt at measuring the diversity of reproductive systems among the tribes, based on relatively simple criteria such as the presence of dioecism, monoecism, and apomixis (Table 1), indicates that all the major systems are present in very few tribes. The most diverse display lies in five tribes: Arundineae, Chlorideae, Eragrostideae, Festuceae, and Paniceae, and a further group of four tribes Andropogoneae, Aveneae, Hordeeae, and Pappophoreae is nearly as variable. However, apomixis is known in only one species in the Hordeeae; dioecism is known only in monotypic *Sohnsia* in the Pappophoreae; these data unduly imbalance Table 1. Deficiencies in the description of the flowers in many genera

make it difficult to interpret the breeding system present, and may be the cause of further imbalance in Table 1.

Among the tribes, and hermaphroditism apart, the most frequently occurring breeding systems are monoecism, including andro- and gynomonoecism, which is known in about 25 tribes, and cleistogamy which is known in about 20 tribes.

REPRODUCTIVE SYSTEMS AND THEIR EVOLUTION

I propose to consider the reproductive systems in the family, and their possible, or even probable, evolution. This will be fraught with difficulties, not the least of which will be problems of finding true relatives, i.e., the correct placing of some genera in tribes, or the incomplete descriptions of flowers of many genera. Occam's razor will have to be used to prevent a plethora of inconsequential pathways.

The assumption that hermaphroditism is basic to the grass flower seems incontestable. Any deviation from hermaphroditism that results in separation of the two sexes—the evolution of various kinds of monoecism and dioecism—is one major departure. It is relatively easy to derive dioecism by postulating a gene for male sterility and another for female sterility, but valid genetic bases for their establishment, and for their maintenance, in natural populations are required as a variety of models show (Charlesworth & Charlesworth, 1978a, 1978b; Lloyd, 1974b, 1975a, 1976; Ross & Weir, 1976). The mutants must find the genetic milieu suitable for fixation or for the development of polymorphism, and develop in dioecism the linkages necessary to control segregation for sex. Similarly, the evolution of self-compatibility from self-incompatibility is easily described, but self-incompatibility must be selected against for self-compatibility to become fixed in a population. Habitual cleistogamy presumes self-compatibility, or at worst, the simultaneous evolution of self-compatibility and of changes in the flowering process.

I have chosen to present the steps that are envisaged in the evolution of any particular breeding system always as steps forward towards that system, i.e., as a progression. That regression is possible, e.g., from dioecism to monoecism by restoration of the alternate sex, is not commented upon unless the evidence suggests that this may have significantly occurred.

SEPARATION OF SEXES

The male and female organs may be separated from the close company of hermaphroditism in a variety of ways, but the simplest expression lies in dioecism and the more complex expression in the various forms of monoecism. Dioecism is less frequent than monoecism in the Gramineae.

MONOECISM, ANDROMONOECISM, AND GYNOMONOECISM

Monoecious plants are those where both sexes occur on the one plant but wholly or partly in different flowers; in monoecism male and female flowers occur on the same plant; in andromonoecism hermaphrodite (perfect) flowers and male flowers occur on the same plant; in gynomonoecism hermaphrodite flowers and

TABLE 2. Monoecism in the tribes of grasses; tribes in the order of Hubbard (1973).

Monoecism[a]	Andromonoecism[a]	Gynomonoecism[a]
	Bambuseae 3,[b]	
Atractocarpeae 3,[b]		
Phareae 1		
Olyreae 1		(Olyreae)
Buergersiochloeae 1		
Parianeae 1		
Centotheceae 3,[b]		Centotheceae[b]
Oryzeae 1		
Phyllorachideae 2		
	Arundineae 3,[b]	
	Danthonieae 3,[b]	
	Arundinelleae 2,[b]	
Isachneae 2,[b]	Isachneae[b]	Isachneae[b]
	Hordeeae 3	
		Festuceae 3,[b]
Aveneae 2,[b]	Aveneae 2,3,[b]	
	Phalarideae 2,3,[b]	
	Pappophoreae 3,[b]	
Eragrostideae 3,[b]	(Eragrostideae)	Eragrostideae[c]
	Chlorideae 2,[b]	
	Zoysieae 1	
Paniceae 2,[c]	Paniceae[b]	
Lecomtelleae 2,[b]		
Andropogoneae 2,[b]	Andropogoneae[c]	Andropogoneae[c]
Maydeae 2		

[a] 1 = 1-flowered, 2 = 2-flowered, 3 = 3- or more-flowered in the genera in which the monoecious states are known.
[b] Sex differentiation within spikelet.
[c] Sex differentiation both within and between spikelets.

female flowers occur on the same plant. The distribution of these systems among the tribes is shown in Table 2 where the tribes are arranged in the linear order of Hubbard (1973).

Because the step from hermaphroditism to andromonoecism or to gynomonoecism demands a single loss of fertility in each, and because both states are seen as pathways to monoecism, they may be considered first.

Gynomonoecism

Gynomonoecism is not frequent in the grasses; it is probably only successful in eragrostoid *Munroa* (Anton & Hunziker, 1978), but is known in a total of 8 genera among the six tribes listed in Table 2, viz., *Centotheca, Coelachne, Diandrolyra, Eriochrysis, Heteranthoecia, Munroa, Piresia, Poa*, (full references in Connor, 1980). For its origin, gynomonoecism demands a loss of male fertility in some flowers, but there must be a decrease in inbreeding to compensate for the reduction in male fertility (Charlesworth & Charlesworth, 1978b). Of the genera listed, there is evidence of self-compatibility only in *Poa*.

Another feature of gynomonoecism is that relatively fewer anthers must provide pollen for a relatively greater number of ovules, a contrast with andromon-

oecism (see p. 58). Anton (1978) gave some examples of the distribution of her-maphrodite and female flowers in Argentinian *Poa*, which show that there may be as few as 1 anther per ovule and up to 1.7 anthers per ovule.

Andromonoecism

Andromonoecism, hermaphrodite and male flowers on one plant, is wide-spread. This system is expressed in two major aspects; in one the two sex-forms occur within a single spikelet, and in the other differentiation for sex-form occurs between spikelets.

Andromonoecism is associated with the trend towards a single hermaphrodite terminal floret, a syndrome which is found in several tribes, but is at its fullest development in the biflowered spikelets of the large tribes Andropogoneae, Arun-dinelleae, and Paniceae.

Andropogoneae.—The Andropogoneae could well be the graveyard of those who wish to interpret the variety of andromonoecism expressed there! At the generic level one may choose between the 20 genera advocated by Roberty (1960) and a current estimate of about 80 genera.

In this tribe spikelets are usually paired, one pedicelled and the other sessile, and each is biflowered. The lower floret is usually neuter and the upper her-maphrodite [in abbreviated form S(OH) + P(OH)][3] but the andromonoecious form [S(OH) + P(OM)] is a common alternative. The range of sex-forms in Table 3 shows that andromonoecism may be expressed in several ways.

The essential first step in the evolution of andromonoecism is a loss of some female fertility; ovules develop a low genetic value, and those flowers become male. This step is said not to be easily established, and the view of Charles-worth & Charlesworth (1978b) is that, within the limits of their model, andro-monoecism is unlikely to evolve as an outbreeding system.

The evolution of andromonoecism in the Andropogoneae would best be seen to have developed along the following pathway. There must first have been the evolution towards biflowered spikelets with hermaphrodite florets; and the de-velopment of paired spikelets. This was followed by the lower florets becoming male through the loss of female fertility. A subsequent mutation affecting the male fertility of those same lower florets would leave an apical hermaphrodite flower in each of the paired spikelets, and thus allow one modal form: S(OH) + P(OH). A further loss of female fertility, this time in the pedicelled spikelet only, would give rise to the andromonoecious form: S(OH) + P(OM). Such progres-sions would be slow to evolve.

The time at which the male and female sterility mutations arise during the evolution of the modal sex-forms allows the development of some of the andro-monoecious variants: S(MH) + P(MH) of *Andropterum* where female sterility alone has operated in the basal flowers; S(MH) + P(OM) of *Sehima* where the sessile spikelets show an uncompleted series of gene actions; and S(MH) + P(MM) of *Robynsiochloa* with even fewer mutations.

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[3] S = Sessile spikelet, P = pedicelled spikelet; H = hermaphrodite; M = male; F = female; O = neuter. Florets of a spikelet are included by brackets and in the order lower, upper. Symbols linked by + indicate presence on the one plant.

TABLE 3. Sex-forms in the Andropogoneae. H = hermaphrodite; M = male; F = female; O neuter. If triads are present there is usually an extra pedicelled spikelet. Homogamous pairs, where present, occur below the pairs shown here, and all flowers are M or O. Based on data from Jacques-Félix, Hubbard, Stapf, Pilger, Clayton.

Spikelet			Spikelet		
Sessile[a]	Pedicelled[a]		Sessile[a]	Pedicelled[a]	
Andromonoecism			Gynomonoecism		
O H	O M	*Elionurus*	O H	O F	*Eriochrysis*
M H	O O	*Kerriochloa*			
M H	O M	*Sehima*			
M H	M M	*Robynsiochloa*			
M H	M H	*Andropterum*			
Monoecism			Hermaphroditism		
M F	O O	*Triplopogon*	O H		*Cleistachne*
O F	O M	*Agenium*	O H	O O	*Bhidea*
M M	O F	*Sclerandrium*	O H	O H	*Erianthus*
M F ⎱ M M ⎰	M F ⎱ F F ⎰	*Lophopogon*			

[a] In each pair the left entry represents lower floret and right the upper floret of spikelet.

Internal evidence for the evolution of andromonoecism in this way in the Andropogoneae is sparse; pairs of spikelets in which both flowers of each are hermaphrodite is reported as a mutant in *Sorghum*, where a dominant gene controls restoration of fertility in flowers otherwise neuter (Webster, 1965). The closest approximation to paired spikelets of totally hermaphrodite flowers is in *Andropterum*: S(MH) + P(MH). The main evidence seems to lie in the presence of basal male florets, even in sessile spikelets (Table 3), indicating that the initial loss of female fertility occurred there. In the development of the spikelet the upper floret grows faster and is always larger (Bonnett, 1966).

Paniceae and Arundinelleae.—The Paniceae show a more general trend towards a reduced form of hermaphroditism because often the upper floret of a spikelet is a lone hermaphrodite flower.

In the biflowered Arundinelleae there is a common pattern of hermaphroditism in the upper floret, and various levels of emasculation and defeminization in the lower florets (Phipps, 1964). Spikelets are not paired in the Arundinelleae, though dimorphic florets are common. The Arundinelleae, it is assumed, followed a one-mutation pathway to andromonoecism because in only the lower floret is there any loss of sexuality.

Self-fertilization or self-compatibility is not very widely documented in the Andropogoneae, even with the inclusion of genera where cleistogamy is recorded (Connor, 1980). For the Paniceae the information is about equal, though *Paspalum* (Burson, 1979) and *Lasiacis* (Davidse, 1979) may be more firmly included as self-fertile genera. In the Arundinelleae there is no information on the compatibility relationship of any taxon; however, the anthers in *Arundinella pumila*, as described by Bor (1955), are very small and suggestive of cleistogamy, but anther length dimorphism occurs in *Arundinella*, e.g., anthers in male florets in *A. holcoides* and *A. ciliata* are about half as long as those in hermaphrodite

flowers. Anther length dimorphism is a feature of andromonoecism (Connor, 1980), but its relationship to self-fertilization or self-incompatibility, or to any aspect of pollination is unknown. On the whole, there may be sufficient self-compatibility to argue the development of andromonoecism in the ways outlined if andromonoecism aids in increased cross-fertilization.

Monoecism

Monoecism, separate male and female flowers on one plant, is exclusive to some tribes (Table 2). No other sex-form occurs in Buergersiochloeae, Lecomtelleae, Maydeae, Parianeae, Phareae, or Phyllorachideae. Monoecism, together with other sex-forms, occurs in: Andropogoneae, Atractocarpeae, Aveneae, Centotheceae, Isachneae, Olyreae, Oryzeae, and Paniceae. In general, a 1- or 2-flowered spikelet is a characteristic associate of monoecism.

In the Atractocarpeae, Isachneae, Aveneae, and some Paniceae monoecism occurs as separate male and female flowers in the one spikelet—perhaps the lowest form of strict monoecism. In the zizanioid Oryzeae, and in many instances in the Andropogoneae, there is separation of spikelets of different sex (see table 3 in Connor, 1980).

Among the bambusoid tribes Olyreae, Phareae, Parianeae, Buergersiochloeae, and Phyllorachideae the arrangement of sexually differentiated spikelets in an inflorescence is varied; thus there may be:

(i) sexes mixed in an inflorescence, often in paired spikelets with sessile female and pedicelled male as in *Maclurolyra* or *Pharus*;
(ii) sexes segregated on one inflorescence, females above and males below as in *Buergersiochloa*;
(iii) sexes completely segregated in pairs of racemes as in *Ekmanochloa*;
(iv) sexes completely segregated with male flowers terminal above, and axillary females below as in *Humbertochloa*.

Internal evidence that a gynomonoecious pathway to monoecism is at least possible in the Olyreae, is available from the work of Soderstrom & Calderón (1974) who showed that pedicelled spikelets with an hermaphrodite organization, and sessile female spikelets occur in *Diandrolyra*, and Bahian *Piresia*. The pedicellate "hermaphrodite" spikelets, however, fall soon after pollen is shed; effectively, monoecism is achieved. Regardless of this precise pattern, the gynomonoecious pathway is evident. Charlesworth & Charlesworth (1978b) describe this system as involving firstly a reduction in male fertility in some hermaphrodite flowers to produce female flowers and thus gynomonoecism, followed by a reduction in female fertility of the hermaphrodite flowers to produce male flowers, a sequence $H \rightarrow H + F \rightarrow M + F$.[4] Correlatively with the sterilities there must be a large reduction in inbreeding. Monoecism is seen by the Charlesworths as an uncommon development in flowering plants, and they emphasize that it may

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[4] H = Hermaphrodite, M = male, F = female; symbols linked by + indicate presence on the one plant.

well be necessary for two or more mutations to reduce female fertility to such an extent that it will yield a male flower. There is no linkage between sterility genes.

Redistribution of male and female flowers into the patterns indicated above would seem to flow easily from a simple, terminal inflorescence of flowers of both sexes to the advanced form of "terminal male and axillary female" inflorescences. This redistribution could be developing during the sequence of mutations eliminating ovule production of those flowers that were still hermaphrodite. Not every known sex-form is accounted for: e.g., in *Lithachne* the axillary inflorescence may contain one apical female-flowered spikelet and several male-flowered spikelets below (Hitchcock & Chase, 1917; Soderstrom & Calderón, 1974), and in *Phyllorachis* the terminal inflorescence bears male flowers above and female flowers below, while the axillary inflorescence is totally female (Hubbard, 1939). These examples and others represent possible phases in the development of monoecism; it is unreasonable to expect evolution conveniently to match every model.

The tribe Maydeae is strictly monoecious; here male inflorescences are found above the female ones, there are sessile and pedicelled spikelets in unisexual pairs, and a tendency towards axillary inflorescences of female flowers. The tribe is alternatively included in the strongly andromonoecious Andropogoneae; any projected pathway to monoecism would seem to be that through andromonoecism, followed by redistribution of male flowers to terminal inflorescences, and with hermaphrodite flowers being distributed below the males, or to axillary positions. A second mutation causing male sterility in the hermaphrodite flowers of axillary inflorescences would produce female flowers only.

In the Zizanieae, or zizanioid Oryzeae, males are present in terminal inflorescences, and females in leaf axils below as in *Luziola*, or are distributed on one inflorescence as female flowers above the male flowers as in *Zizania*. The pathway to monoecism is expected to be the same as that for the bambusoid tribes, though there is no internal supporting evidence; and *Zizania latifolia* by not conforming exactly to the "female above, males below" diagnosis but in having inflorescences less perfectly arranged (Bannikova, 1976), in fact offers some evidence that sex-forms are being redistributed. The Zizanieae are self-fertile (East, 1940), but protogynous (Weir & Dale, 1960).

Monoecism with the sexes differentiated within a spikelet involves the same genetics as the other monoecious forms. Between-floret differentiation occurs in the Atractocarpeae, Centotheceae, Eragrostideae, Isachneae and Lecomtelleae, in one or two genera of the Andropogoneae, and Argentinian *Hierochloe* (Aveneae).

In both the Centotheceae and the Atractocarpeae there are several florets per spikelet. The sex-forms in the Centotheceae range from hermaphroditism through gynomonoecism to monoecism as in: *Orthoclada* H; *Centotheca* H + F; *Calderonella* M + F and *Zeugites* M + F. In *Zeugites* and *Calderonella* the lowest floret only is female; but in *Centotheca* the upper floret is female. Neuter flowers may be present in some members of the Centotheceae, so that in *Chevalierella* the lowest floret is hermaphrodite and the upper neuter; in *Chasmanthium* the two lowermost florets are neuter and the remainder hermaphrodite. The internal evidence from *Centotheca* would point to a gynomonoecious origin of monoecism.

Blepharidachne (Eragrostideae) has three monoecious species and a fourth, *B. kingii*, which is hermaphrodite. The pathway here to monoecism is via andromonoecism. Only one seed is formed in the four-flowered spikelet—that in the penultimate floret which has a functional gynoecium. Anthers may number 1 or 2 or 3 depending on the species (Hunziker & Anton, 1979). In *Atractocarpa* and *Puelia* the female flower is apical in the spikelet, the flowers below being male and/or neuter; most related bambusoid genera have hermaphrodite flowers. *Hierochloe* (Aveneae) in Argentina is monoecious (De Paula, 1975), but most species in that genus are andromonoecious. Andromonoecism is the appropriate pathway to monoecism in these genera.

In the group of related tribes Isachneae, Lecomtelleae, and Paniceae, sex differentiation mostly occurs within the spikelet: usually the lower flower is male and the upper female, though in *Lecomtella* there are some spikelets with two male florets and others with one male and one female flower. In the Isachneae because gynomonoecism is present as in *Coelachne* and *Heteranthoecia* (p. 51), and andromonoecism in some species of *Isachne* (Bor, 1952), there is internal evidence of two possible pathways to monoecism. *Lecomtella*, with an excess of male flowers in some spikelets (Stapf, 1927), may represent what Charlesworth & Charlesworth (1978b) refer to as a reduction in female fertility through a mutation increasing the ratio of male to female flowers, making the bisexual form more malelike. Such a character is indicative of an andromonoecious origin. But the Lecomtelleae is a tribe distant from the main stream of evolution in the Paniceae (Brown, 1977), and it would be unwise to transfer too much influence from it to the Paniceae. In the Paniceae, *Chamaeraphis* and *Pseudoraphis* are monoecious. An andromonoecious pathway is indicated for members of these tribes. *Hygrochloa*, aquatic, monoecious, newly recognized, and the only genus in the Paniceae with male and female spikelets separately distributed on the inflorescence, is of remote affinity in the tribe according to Lazarides (1979).

Redistribution of sex-form is associated with the most highly developed forms of monoecism; the change from a shoot with a terminal inflorescence to one incorporating axillary inflorescences as well, seems one opportunity in the evolution of monoecism. It necessitates a particular morphogenesis, but it seems to be the next most successful evolutionary step in inflorescence development. It is also a very deliberate step towards the possibility of dichogamy—one feature that can be associated with attempts to promote allogamy.

The evolutionary pathways to monoecism backed by genetic models of Charlesworth & Charlesworth (1978a, 1978b) seem not unreasonable even though they are heavily weighted in the direction of the avoidance of inbreeding by promotion at least of some way of ensuring outcrossing.

Among the monoecious tribes, self-compatibility is known in the Andropogoneae, Aveneae, Eragrostideae, Maydeae, and Paniceae, but nothing is recorded of the compatibilities of the Buergersiochloeae, Centotheceae, Olyreae, Parianeae, Phareae, and Phyllorachideae (see list in Connor, 1980). Self-compatibility and the associated inbreeding depression are seen by Charlesworth & Charlesworth (1978a, 1978b) to be essential to the pathways they outlined. There is sufficient self-compatibility to satisfy that requirement. Should any of these mon-

oecious genera be self-incompatible, alternative genetic explanations must be sought.

Excess Maleness

"Chez beaucoup d'espèces tropicales et surtout chez les Andropogoneae, comme leur nom l'indique, il y a androphilie c'est-à-dire nette prédominance des éléments mâles" (Jacques-Félix, 1962). Clifford (1961) might see these extra anthers as offsetting a reduction to three stamens per flower, because for a wind-pollinating group this common reduction is seen to be disadvantageous. Cruden (1977) and other authors would refer to this in general as producing very high pollen-ovule ratios. Charlesworth & Charlesworth (1978b) might see this predominance of male flowers as part of a projected sequence towards monoecism and/ or dioecism where at some stage plants are "more malelike" in that they possess many male flowers. The loss of the ovule function suggests that pollen is of high genetic value and that there have been substantial increases in male fertility; both these are anticipated from their models.

In the Andropogoneae the size of the increase in male fertility is measurable in some taxa in two ways: (i) the number of solely male flowers relative to her-maphrodite flowers and (ii) the relative sizes of the anthers found in both. Neither of these is the pollen-ovule ratio of Cruden though they contain its essentials. Differences in size of anthers, depending in which flower they occur, are given for *Diheteropogon, Exotheca*, and *Hyperthalia* by Connor (1980). *Euclasta con-dylotricha* is also described as dimorphic for anther size, those of the male flower being much longer than those of the hermaphrodite flower (Jacques-Félix, 1962); I am unable to find any absolute measurements. There must be other equivalent data for the tribe though I am unaware of them.

The relative number of anthers per ovule in a pair of spikelets can be readily calculated from data in Table 3. For many genera with the form S(OH) + P(OM) there are three anthers in the male flower and three in the hermaphrodite flower to 1 ovule, i.e., 6 a : 1 ov. From the form S(OF) + P(OM) the ratio is 3 a : 1 ov, as is the ratio in forms with pairs S(OH) + P(OH).

Where there are pairs of homogamous male spikelets subtending the "fertile" part of an inflorescence, there is an immediate increase in anther : ovule ratio. Thus in a genus like *Elymandra* in one raceme with three ovules there may be something of the order of 28 to 46 anthers—a range of 9 a : 1 ov to 15 a : 1 ov (see fig. 240 in Jacques-Félix, 1962). Where anther size polymorphism occurs as in *Hyperthelia edulis* (Hubbard, 1950 as *Hyparrhenia*) each ovule in a raceme is accompanied by three anthers up to 9 mm long in the sessile spikelet, six anthers up to 19 mm long in the pedicelled spikelets, and six anthers up to 4 mm long in the homogamous pair. In *H. colobantha*, the upper raceme of the pair is reduced to one pedicelled, male spikelet (Clayton, 1967); the ratio here becomes 18 a : 1 ov for the two racemes. Clayton did not describe anther sizes.

The data in Weatherwax (1926) for Oriental Maydeae give anther : ovule ratios for: *Chionachne* 12–20 a : 1 ov, *Coix* 180–600 a : 1 ov, *Polytoca* 30–60 a : 1 ov.

Among the tropical Bambusoideae monoecism is well established in the Oly-reae; Soderstrom & Calderón (1979a) and Calderón & Soderstrom (1973) indicate

the frequencies of male and female flowers in some genera. In *Maclurolyra* for example, the terminal inflorescence bears one female flower and close by 4–6 males giving 12–18 a : 1 ov, and below these may be several pairs of spikelets with one female and one male flower each, i.e., 3 a : 1 ov. *Bulbulus* is similar; (this genus has been renamed *Rehia* by Fijten, 1975). In *Arberella flaccida* the ratio is 15–24 a : 1 ov, in *A. costaricensis* 24–30 a : 1 ov, in *A. dressleri* 18–24 a : 1 ov.

In *Strephium* and *Raddia*—where the two sexes are borne on separate inflorescences—there are many more male flowers than female in *Strephium*, but fewer male flowers than female inflorescences in *Raddia*.

Pariana, the monotypic genus of the Parianeae, may bear 75–105 a : 1 ov, or even more.

For cross-fertilization pollen must firstly reach a receptive stigma, only then can the compatibility specificity be expressed. Wind-pollination is a very unspecialized pollination system and in the Gramineae is linked to an efficient and specialized incompatibility system. High pollen : ovule ratios are characteristic of anemophily. The Andropogoneae, Olyreae, and Maydeae that have been discussed, all possess high or relatively high, anther : ovule ratios (the precise pollen : ovule ratios I am unable to calculate). Yet the Maydeae are self-fertile (East, 1940) and so are many species of the Andropogoneae.

For the tropical Olyreae, wind pollination is very difficult because of the extreme stillness of their forest floor habitat (Davis & Richards, 1933; Whitehead, 1969; Soderstrom & Calderón, 1971, 1979b); further, the leaves cover or protect the abundant axillary inflorescences, limiting what wind action there is. For the herbaceous bambusoids, therefore, the excess of male flowers may be the guarantor of pollination by an inadequate anemophily or by the secondary development of entomophily.

This explanation cannot be applied to the Andropogoneae of the savanna and of tropical areas elsewhere as far as I know. The Andropogoneae may just need abundant pollen to overcome problems of effective wind pollination; if so, they differ significantly in this respect from many other grasses.

DIOECISM

Dioecism is not a major phenomenon in the Gramineae, as dioecious species are known from 20 oligotypic genera only. Among the tribes, dioecism is found in the Aeluropodeae, Arundineae, Chlorideae, Eragrostideae, Festuceae, Paniceae, and Pappophoreae (Table 4). Gynodioecism, a specialized form of dioecism, if included here does not alter the number of tribes with dioecious taxa. Two tribes are significantly dioecious, the Aeluropodeae and the Chlorideae; in the former there are five dioecious genera and in the latter there are seven. Elsewhere one or two genera in large tribes is characteristic, e.g., *Spinifex* and *Zygochloa* are the only two dioecious genera in the Paniceae (Blake, 1941), and only *Neeragrostis* (Nicora, 1962) and *Scleropogon* (Reeder, 1969) in the Eragrostideae.

In most genera with dioecious taxa the spikelets are multiflowered; exceptions are the two biflowered panicoid genera *Spinifex* and *Zygochloa*; none is singleflowered.

For the Arundineae where *Gynerium* is dioecious and *Lamprothyrsus* has

TABLE 4. Dioecious genera; references in Connor (1980).

Aeluropodeae:	*Allolepis, Distichlis, Jouvea, Monanthochloe, Reederochloa.*
Arundineae:	*Cortaderia,*[b] *Gynerium, Lamprothyrsus.*
Chlorideae:	*Bouteloua,*[b] *Buchloe,*[a] *Buchlomimus, Cyclostachya, Opizia,*[a] *Pringleochloa,*[a] *Soderstromia.*[a]
Eragrostiaeae:	*Neeragrostis, Scleropogon.*
Festuceae:	*Festuca* (subgenus *Leucopoa*),[c] *Poa.*[a,b]
Paniceae:	*Spinifex, Zygochloa.*
Pappophoreae:	*Sohnsia.*

[a] Occasionally monoecious.
[b] Also gynodioecious.
[c] Correcting entry in table 1 of Connor (1980).

been so at some time—and gynodioecism is active in *Cortaderia* (Connor, 1974)—a gynodioecious pathway to dioecism is evident. Andromonoecism is also present in the tribe in *Phragmites* and *Gossweilerochloa*; *Gossweilerochloa*, a monotypic genus from Angola has lower florets hermaphrodite and upper florets male (Renvoize, 1979). Neither it nor *Phragmites* persuades me that a route through andromonoecism to monoecism and thence to dioecism is likely in the tribe.

The suggested pathway towards dioecism in the Arundineae via gynodioecism involves firstly the establishment of male sterility gene(s)—usually recessive—in some hermaphrodite plants giving rise to hermaphrodite and female plants, i.e., gynodioecism. This is followed by a mutation—usually dominant—for female sterility which acts in the hermaphrodites thus giving male plants. Such a combination of alternating gene action will lead to sets of linked genes controlling sex, and to heterogametic male plants. Charlesworth & Charlesworth (1978a) emphasize that this process is a long and extremely slow one. Also important is that self-compatibility and a high level of self-fertilization occur in the group where evolution of dioecism is taking place, and that there is some increase in pollen output by the males. In New Zealand species of *Cortaderia*, at least, there is abundant self-compatibility in hermaphrodite plants (Connor, 1974).

The tribe Chlorideae offers perhaps the greatest concentration of dioecious genera, but Reeder (1969) pointed out that with the exception of *Buchlomimus* and *Cyclostachya*, plants of *Buchloe, Opizia, Pringleochloa,* and *Soderstromia* may at times be monoecious. Systems currently known in the Chlorideae, apart from dioecism, include hermaphroditism, andromonoecism, and possibly gynodioecism in *Bouteloua chondrosioides* (Reeder & Reeder, 1966; Reeder, 1969). On the basis that monoecism is recurrent among the dioecious taxa (Reeder, 1969), the probable pathway to dioecism for the Chlorideae is through monoecism, that is, along pathways to monoecism that have already been discussed (p. 54). It is clear that this pathway is much longer than the gynodioecious one, necessitating firstly the development of andromonoecism as the consequence of reduction in female fertility in some flowers, and subsequently a further reduction in male fertility of the remaining hermaphrodite flowers to produce female flowers and thus the monoecious state. As was discussed earlier (p. 52), low genetic values in the ovules of the hermaphrodite flowers that become male is the major factor. Subsequent steps producing more malelike and more femalelike phenotypes ultimately yield the male and female plants of a dioecious population. Dioe-

cism originating in this way will be controlled by sets of linked genes and be the result of an extremely slow evolutionary process. Genetic conditions and selection pressures under which such systems could evolve are detailed by Charlesworth & Charlesworth (1978b). In taxa following this sort of pathway, males and females with traces of the activity, not just the morphology, of the opposite sex may be found (Lloyd, 1975b). In the Chlorideae cleistogamy is common and may be one of the self-fertilizing systems being selected against by dioecism.

In the closely related Eragrostideae there are two dioecious genera, *Neeragrostis* and *Scleropogon*. There is internal evidence from within the tribe to indicate a pathway towards dioecism, and the proposition of an escape from inbreeding is quite strong, because self-compatibility and cleistogamy are well established there (see table 8 in Connor, 1980). *Ectrosia*, which is commonly cleistogamous, may have a large number of male flowers—making it andromonoecious—or those flowers may be neuter (Hubbard, 1936). *Munroa* is gynomonoecious in most species; *Blepharidachne*, on the other hand, is hermaphrodite in one species and monoecious in three others; on these bases, pathways through monoecism are probable for the dioecious genera.

The gynomonoecious origin of dioecism differs only in initial detail from the andromonoecious pathway just described for the Chlorideae. Initially a male sterility gene acts in some flowers to produce plants with female and hermaphrodite flowers. Subsequent steps invoke female sterility in the hermaphrodite flowers to produce monoecious plants; from then on the process is that described above. The difficulties alluded to by Charlesworth & Charlesworth (1978b) are unchanged by the chronology of genes reducing fertility.

In the Aeluropodeae five genera (or more) are dioecious (Table 4). Yet there is no internal evidence to suggest a pathway to dioecism; *Aeluropus* itself is hermaphrodite. The Pappophoreae are distinguished on the other hand by hermaphroditism except for the monotypic dioecious genus *Sohnsia* for which no clear pathway to dioecism is indicated from the floral forms of other genera in the tribe; what is clear is that cleistogamy is a feature of many pappophorean genera (Connor, 1980).

For *Poa* (Festuceae) pathways to dioecism are not difficult to suggest, though none is explicit from internal evidence. In *Poa* there are gynodioecious species which would suggest this direct pathway, but gynomonoecism is also present and suggests that the much longer monoecious pathway is possible. The choice may lie in recognizing that two pathways could operate. In *Festuca*, subgenus *Leucopoa*, there is sporadic dioecism; no particular pathway is evident.

In the Paniceae *Spinifex*, and its segregate *Zygochloa*, are the only dioecious genera; they are also the only dioecious genera in the subfamily Panicoideae. The floral arrangement in the biflowered Paniceae—lower floret male or very often neuter, upper floret hermaphrodite—indicates andromonoecism or alternatively hermaphroditism. A possible pathway to dioecism could involve either monoecism or gynodioecism. Monoecism is a low frequency phenomenon in the tribe, occurring in *Hygrochloa*, *Chamaeraphis* and *Pseudoraphis* only. Gynodioecism is unknown. The gynodioecious pathway is simpler than the monoecious one because the action of the necessary genes seems more direct, but simplicity is unlikely to be the guarantor of an evolutionary pathway.

The pathways that have been discussed as being the most probable in the evolution of monoecism and dioecism depend to a large extent on the presence of self-compatibility and self-fertilization. This may appear to suggest that self-compatibility was, or is, very widespread in the family. It is. But if the predecessors of 20 dioecious genera and of 45–50 monoecious genera evolved as a reaction to self-compatibility, that number is very small relative to the 600–700 genera in the family.

Willson (1979), who does not accept that the advantages of obligate outcrossing "... present as powerful and all pervasive a force as seems to be commonly assumed," described an ecological gradient towards dioecism. Sexual selection along one gradient is seen ultimately in an "... overwhelming reproductive success of some individuals functioning as say, males; selection then would favor the allocation of food resources entirely to male flowers and increase their success still further." Genetic advantage to dioecism is not excluded, and Willson suggests that both genetic diversity from recombination, and sexual selection were contributors to the evolution of dioecism.

HERMAPHRODITISM

Variation in the breeding system of hermaphrodite plants is achieved at the genetic level by mutations affecting compatibility relationships, and at another level by changes in the timing of presentation of pollen and of receptive stigmata. Dichogamy does not invariably guarantee a within-plant delay in the maturation of male- and female-bearing organs or in their presentation, often because of the sequential emergence of inflorescences on the one plant (see Burton, 1974).

An important evolutionary step in the family is the development of self-compatibility, a step independent of changes in levels of ploidy (Lundqvist, 1975). Self-compatibility has been identified in about 100 genera in the family (Connor, 1980).

CLEISTOGAMY

Self-fertilization is extensively used as a normal method of reproduction especially in annuals (Stebbins, 1957), and in the specialized form of cleistogamy, self-fertilization has been reported in 18 tribes and from about 70 genera (table 8 in Connor, 1980). This is most probably an underestimate if one judges from the illustrations of so many flowers, and from the anther sizes given in some descriptions. Mostly cleistogamy is facultative, though some taxa are predominantly cleistogamic and some few are known only in the cleistogamic form. Some tribes have greater concentrations of cleistogamous genera than others, e.g., in the Eragrostideae 11 genera bear cleistogamic flowers, and there are 9 genera in the Paniceae, 7 in the Andropogoneae, and 6 in each of the Aveneae, Danthonieae, and Festuceae.

The evolution of cleistogamy depends initially on the presence of self-compatibility. Morphological features often associated with nonanthesis, e.g., reduced anther and lodicule sizes, or even the loss of lodicules, are probably interpretable as precocious development (Lord, 1979). In addition to cleistogamous flowers in terminal inflorescences, cleistogamous inflorescences may be hidden

in leaf axils—the cleistogenes of Chase (1918) which I prefer to call clandestine inflorescences or spikelets.

Clandestine inflorescences are smaller than aerially borne inflorescences, and in the most reduced form are single spikelets only; they are probably precociously developed, because in *Stipa leucotricha* Dyksterhuis (1945) could record them in plants about six months old. In the same species he found that clandestine spikelets were advanced in seed setting before anthesis had begun in aerial inflorescences.

This specialized form as clandestine spikelets is more advanced than facultative cleistogamy in aerial inflorescences. In all known examples they are a secondary form of seed setting, but usually produce in total fewer seeds than aerially borne inflorescences, though as Hubbard (1933) pointed out, clandestine spikelets may occur in all leaf axils of *Cleistochloa*; in *Microlaena polynoda* very many leaf sheaths are swollen with spikelets (Connor & Matthews, 1977).

Clandestine axillary spikelets are known in 13 genera, viz., *Aristida, Calyptochloa, Cleistochloa, Cleistogenes, Cottea, Danthonia, Diplachne, Enneapogon, Microlaena, Muhlenbergia, Sieglingia, Stipa, Triplasis*; full references are in Connor (1980). Aerial inflorescences in all these genera bear both cleistogamic and chasmogamous florets, except *Cleistochloa* where only chasmogamic flowers are known (Hubbard, 1933).

At another level of development, cleistogamy is found in subterranean spikelets; these spikelets are most probably more highly evolved than those that arise from the conversion of an axillary vegetative bud to a reproductive one as in clandestine spikelets. Subterranean spikelets are reported from four genera only: *Chloris* (Chlorideae), *Amphicarpum* and *Paspalum* (Paniceae) and *Eremitis* (Parianeae). In *Eremitis* these subterranean spikelets were only recently discovered (Soderstrom & Calderón, 1974), but the well-known annual *Amphicarpum purshii* was subject to experiment by McNamara & Quinn (1977) who showed the high level of dependence by this taxon on subterranean spikelets.

Cleistogamy was suggested by Clifford (1961) as one possible response following a change from entomophily to anemophily in the Gramineae. For cleistogamy to develop the sole requirement is that it must be preceded by a mutation to self-compatibility; this mutation and the development of ancillary features of the cleistogamic habit were unlikely to be simultaneous.

Cleistogamy occurs in plants at both high and low latitudes, at high and low altitudes, in forest and grassland, in annuals and perennials, in archaic tribes and in advanced tribes, in tribes significantly associated with monoecism and dioecism and in tribes that are not. Cleistogamy is known to be a response to differences in daylength, to be a response to soil moisture variation, to co-occur simultaneously with chasmogamy in the same plant, to have differing modes of pollination, and to occur before or after inflorescence emergence. Many of these responses coincide with ecological demands, but ecological or ecophysiological interpretations do not totally account for all occurrences of cleistogamy and certainly not for simultaneous cleistogamy and chasmogamy on the one plant.

Cleistogamy, like other breeding systems, is one evolutionary possibility open to the grasses; they adopted it as a specialized self-compatibility system and later

adapted it in the form of axillary clandestine spikelets, and to a lesser extent in subterranean spikelets. Its frequency is a measure of its success.

APOMIXIS

Departures from and variants on hermaphroditism are pathways open to the grasses, and a departure from sexual reproduction yet another. I do not propose to discuss proliferation though it is important at high latitudes, and intend only very briefly to discuss apomixis because one either discusses embryological detail, or environmental control, or the genetics of inheritance, or invariability in the next generation. All these topics have been most adequately treated elsewhere (Stebbins, 1941; Gustafsson, 1946–1947; Nygren, 1954, 1967; Battaglia, 1963; Connor, 1980).

The distribution of apomixis in the grasses (Table 5) is of no significant value in any systematic interpretation of tribes or lesser ranks. In the Andropogoneae, Paniceae, and closely related tribes, apomixis has been reported in about 20 genera, something of the order of 10% of the genera.

It is significantly absent, or unrecorded, in the Bambusoideae as interpreted by Soderstrom & Calderón (1979b). The Arundinoideae, which always seems central to any discussion on the family, includes two apomictic genera; there are three in the Festucoideae, and three in the Chloridoideae-Eragrostoideae.

At the genetic level, somatic apospory is more frequent in the Panicoideae than elsewhere, but neither it nor gonial apospory (diplospory) is exclusive to any subdivision of the family. The absence of pollen stimulation, i.e., nonpseudogamy, is known only in the five nonpanicoid genera: *Calamagrostis, Cortaderia, Lamprothyrsus, Nardus, Poa*; autonomous apomixis is a more independent state than pseudogamy but possesses little scope for versatility.

Apomixis is associated with monoecism in *Tripsacum* only, and with dioecism in the special cases where females alone are now known—*Cortaderia* and *Lamprothyrsus*. Apomixis occurs in self-incompatible and self-compatible hermaphroditic flowers. In the Andropogoneae it has often replaced andromonoecism. Apomixis is clearly a recent development in the Gramineae and coincident with the universal observations of hybridization and polyploidy.

In many genera apomixis is readily reversible with sexual reproduction because apomixis is rarely totally obligate. Such a capability seems more advantageous than that in the nearest approximation, that is, in the switch from cleistogamic to chasmogamic flowering. Whether the reversals from dioecism as reported for the Chlorideae by Reeder (1969), or any other reversal, is as frequent or as balanced as the sexual-asexual switch among apomicts is unknown.

RESPONSE TO THE BREEDING SYSTEMS

Is there an optimal breeding system for the Gramineae? The question contains a teleological element, but teleology is necessary to allow the formulation of satisfactory hypotheses. Theory suggests two possibilities for maximum heterozygosity, for recombinants, and for maximum capacity to react to major environmental changes; these are dioecism and multiallelic incompatibility genes—

TABLE 5. Apomixis in the tribes of grasses; tribes in the order of Hubbard (1973); references in Connor (1980). + = present; − = absent; SI = self-incompatible; SC = self-compatible; MS = male sterile.

Tribe	Apospory Gonial	Apospory Somatic	Pseu-dogamy	Genera	Sex-Form
Arundineae		+	−	2; *Cortaderia, Lamprothyrsus*	in MS only
Hordeeae	+		+	1; *Agropyron*	hermaphrodite; SC
Festuceae	+	+	+/−	1; *Poa*	hermaphrodite or MS
Aveneae		+	+	1; *Hierochloe*	andromonoecious
Agrostideae	+		+/−	1; *Calamagrostis*	hermaphrodite; SI, SC
Nardeae	+		−	1; *Nardus*	hermaphrodite or MS
Eragrostideae	+		+	1; *Eragrostis*	hermaphrodite
Chlorideae		+	+	2; *Bouteloua, Chloris*	hermaphrodite; SI
Paniceae	+[a]	+	+	9; *Cenchrus, Panicum,* etc.	andromonoecious or hermaphrodite
Anthephoreae		+		1; *Anthephora*	andromonoecious
Andropogoneae	+[b]	+	+	9; *Bothriochloa, Dichanthium,* etc.	andromonoecious
Maydeae	+		+	1; *Tripsacum*	monoecious

[a] Reported in *Paspalum* only.
[b] Reported in *Saccharum* only.

the *S* genes. Other systems seem less adequate on a variety of grounds. Heterostyly is absent.

In the evolution of the breeding systems discussed so far, there is a strong element of the avoidance of self-fertilization especially through monoecism, including andromonoecism and gynomonoecism, and protandry and protogyny in hermaphrodite flowers. Monoecism of itself is not necessarily a breeding system that promotes the avoidance of self-fertilization because self-fertile taxa will remain self-fertile after the evolution of monoecism. Monoecism increases the opportunity for dichogamy but does not generate it.

Andromonoecism is established in one of the more successful groups of the world's grasses, the Panicoideae; the andromonoecious habit has no special merit as a breeding system unless increased male fertility, measured in terms of pollen production, is demanded by the genetic situation. In the Andropogoneae the tendency to become exceedingly male, and consequently with fewer seed-bearing florets, is one of the significant enigmas of the tribe (Clayton, 1967; Olorode & Baquar, 1976; Connor, 1980). Charlesworth & Charlesworth (1978b) do not see andromonoecism evolving as an outbreeding device.

Gynomonoecism, occuring only sporadically in five or six tribes, has only been studied as a breeding system in *Poa annua* (Ellis et al., 1971; Ellis, 1974). Without strong dichogamy, self-fertilization is unlikely to be totally avoided. Gynomonoecism has its main significance as one point on an evolutionary pathway to monoecism, but the evidence from within the tribes in which monoecism occurs, does not suggest that any of the highly evolved monoecious sex-forms is related to currently gynomonoecious groups except in *Diandrolyra* (see p. 54).

Hermaphroditism is very often associated with self-compatibility, and experimentally verified self-fertilization without significant inbreeding depression has

been established in 45 genera; to these must be added those genera where cleis-
togamy is easily verified, bringing the total to about 100 genera (see Connor,
1980). In many of these genera there are self-incompatible species as well, e.g.,
in *Bromus, Lolium, Phalaris,* and *Poa.* It is sufficient to indicate that the mutation
to self-compatibility is, or was, a frequent development, and because this derived
self-compatibility is present in simple and advanced tribes, it may be assumed
that the tendency to mutate is not much younger than the tribes themselves.

Apomixis is generally interpreted as a system lacking evolutionary advantage,
but as it is more frequently facultative than obligate, there are opportunities for
the formation of new recombinants. Should mitotic recombination as discussed
by Stern (1936), Evans & Paddock (1976), and Harrison & Carpenter (1977) be
of widespread occurrence, some of the opprobrium attached to apomixis may be
withdrawn, and this system may be admitted into the group of genetically diverse
reproductive systems.

Best suited to anemophily as the pollen dispersal system, and to the require-
ment for the maximum number of recombinants, are dioecism and multiallelic
incompatibility.

DIOECISM

Dioecism leaves little option but for obligate cross-pollination; the assumption
is usually made that all pollinations are compatible. In strict dioecism each sex-
form makes an equal genetic contribution to the next generation, but there must
also be: (i) chromosomal sex determination, or its equivalent, (ii) an efficient
pollen transfer mechanism, and (iii) a normal sex-ratio. Should there be an eco-
logical differentiation favoring one sex over the other as shown by Freeman et
al. (1976) for *Distichlis spicata* and for other families by Lloyd & Webb (1978),
then the distribution of the sex-forms, both in number and place, may affect the
efficiency of dioecism.

Dioecism in the Gramineae is at a low frequency—about 20 genera from seven
tribes. The genetics of dioecism is unexplored in the family. One count of males
and females in *Buchloe dactyloides,* that of Schaffner (1920), whose results in-
dicated .50M : .50F in the field, this together with a small sample of seed giving
.50M : .50F, constitute the major published facts of dioecism. Voigt et al. (1975)
indicated that with selection a high frequency of female plants could be obtained
in *B. dactyloides* but presented no details. Based on quadrat counts of inflores-
cences, frequencies in the rhizomatous grass *Distichlis spicata* are: .49M : .51F,
but the sexes are not distributed at random (Freeman et al. 1976). In *Bouteloua
chondrosioides* .31M : .69F was obtained from seed (Reeder & Reeder, 1966);
this is a very wide departure from .50M : .50F. Should *B. chondrosioides* be
gynodioecious these valuable results are uninterpretable because of the uncer-
tainty about the sex-form of the seed parents. There is no doubt, however, that
there is an excess of female plants—57M and 118F—among the three families
raised from seed; Lloyd (1974a) discusses the topic of female predominant sex-
ratios.

Differentiation associated with dioecism is better known. There are, for ex-
ample, more florets per spikelets in male plants than in females in *Jouvea* and

Monanthochloe (Villamil, 1969; Weatherwax, 1939), and the greater number of male florets is assumed to be related to the supply of pollen to female spikelets that are hidden among the leaves. In *Jouvea* the males are borne well above the leaves, but in *Monanthochloe* the male flowers, like female flowers, are hidden. The fit to the model is imperfect.

The less specialized form of dioecism, gynodioecism, is restricted to two genera, *Cortaderia* and *Poa*, but there are three genera if *Bouteloua* is admitted. In *Poa* there is an array of species (see summary in Connor, 1980); in *Cortaderia* there are about 20 gynodioecious species and 5 that are apomictic (Connor, 1974; Philipson, 1978; Costas-Lippmann, 1979).

In *Cortaderia* hermaphrodite plants are heterogametic. Some hermaphrodites are self-compatible, but South American *Cortaderia selloana* behaves for the greater part as a dioecious species. Hermaphrodites are self-incompatible, and at most produce a few, poorly germinable seeds; their contribution to subsequent generations is chiefly as pollen parents. Natural populations do not depart from .50M : .50F. The genetics of male sterility are complex, though the behavior in natural populations is simple; thus .50M : .50F is reproducible in nature because female plants are pollinated by plants themselves derived from crosses of the same kind, and therefore heterozygous. Both Lloyd and I (Connor, 1974; Lloyd, 1976) have shown how .50M : .50F is maintained in natural populations.

Male-fertility is dominant over male-sterility, and it is possible in experiments to produce populations of male plants. In some experimental crosses, however, the frequency of females may be greatly in excess of the 50% so commonly found in my experiments and in natural populations (Connor, 1974), and reach 80%. I have no ready genetic model to fit these data, but am attracted on the one hand to explanation for imbalanced sex ratios based on meiotic drive (see Sweeney & Barr, 1978; Hastings & Wood, 1978), and on the other, to cytoplasmic interaction.

This discussion of a subdioecious species is to present data of the kind that is needed for dioecism. Elsewhere I have discussed the self-compatible and strictly gynodioecious New Zealand species of *Cortaderia* (Connor, 1965, 1974).

The small number of dioecious taxa and their distribution among tribes may be an indication that dioecism has been found wanting as an evolutionary possibility within the family. Relative to other families where dioecism is present, dioecism in grasses—about 3% of the genera—is at a low frequency. The greatest concentration of dioecious grasses is in the New World (Reeder, 1969), and it will be interesting to see if the ecological selection for dioecism suggested by Willson (1979) can be invoked to explain any features associated with this pattern; some features of distribution of the taxa are clearly related to major ecological characters.

Gynodioecism is so rare in the family as to not merit much attention as an optimal breeding system. On a pathway to dioecism, such as is discussed by Charlesworth & Charlesworth (1978a), Lloyd (1974a, 1974b, 1975a, 1976), Ross (1970, 1978), Ross & Shaw (1971), Ross & Weir (1976), and Webb (1979), gynodioecious grass is of some evolutionary interest; as a result of occasional but nonpersistent male sterility in many species it is of some interest to plant breeders.

INCOMPATIBILITY

Lundqvist in 1954 demonstrated the genetics of self-compatibility in *Secale cereale*, and in later papers he showed that the system occurred widely enough in the family to be considered the grass or *S-Z* system (Lundqvist, 1955, 1962, 1965, 1969). Work in *Briza, Phalaris* and other grasses has been in full agreement (Hayman, 1956; Murray, 1974); in *Lolium* Hayward & Wright (1971) and Spoor (1976) obtained some inconsistent results, but Cornish et al. (1979a) obtained an orthodox fit to the grass system.

Incompatibility in the Gramineae is unique and its characters include: (i) 3-nucleate pollen (Brewbaker, 1957); (ii) dry stigmas (Heslop-Harrison & Shivanna, 1977); (iii) action for the most part, but not exclusively, on the stigmatic surface; (iv) two independent multi-allelic *S* loci (*S* and *Z*) with functional dependence in a complementary and cooperative action such that the presence of an identical specificity, e.g., S_1Z_1 in both the pollen and the stigma, results in incompatibility (Lundqvist, 1975). Most of these characters are those recorded where incompatibility is sporophytically controlled, but incompatibility in the Gramineae is gametophytic. Figures 8 and 9 in de Nettancourt (1977) clearly demonstrate the compatibilities and incompatibilities of the system.

Lundqvist (1975, et praec.) considered that the *S-Z* system had arisen by duplication of a one-locus system. Pandey (1977, 1980), who considers that the complementary incompatibility system is a secondary one derived from the primitive one-locus multiallelic system, accepts duplication of an *S*-gene as one major part of the evolution of the two-loci system. He envisages firstly the breakdown of the original self-incompatibility and the development of self-compatibility. This is followed by the reintroduction of self-incompatibility genes through recurrent inter- or intraspecific hybridization, and after selection against *S* competition and dominance to allow these fundamental characters of this system to evolve, a duplicate, independently acting self-incompatibility locus is acquired. Self-incompatibility has reevolved, though the characteristics of the system are now novel and may be less efficient than the original system. Charlesworth & Charlesworth (1979) consider that the grass system is most likely to have arisen when ". . . a variety of (allelic) specificities is initially present without causing an incompatibility reaction, and that selection acts on loci (other than the *S* locus) which affect the chance that pollen which matches an allele in the stigma-bearing plant will be rejected."

Lundqvist (1975), de Nettancourt (1977), and Pandey (1977) emphasize the benefit of the bifactorial system of the grasses over the monofactorial system common to many other families. Because the number of specificities in a population is the product of the number of segregating alleles in each locus, the two-loci system ". . . confers on the population a reduction of cross-incompatibility between plants and a minimized risk of random loss of members of its valuable pool of incompatibility genes" (Lundqvist, 1975). Recent contributions to the genetics of the two loci are from Charlesworth (1979) and from Cornish et al. (1979b).

The grass incompatibility system prevents fertilization between genotypes identical in incompatibility alleles, and like other incompatibility systems protects

and regenerates itself. Advantages are reflected in recombination and reconstitution; and for the Gramineae if these qualities are desirable, they are achieved by the retention of a versatile, advanced incompatibility system.

This efficient incompatibility system has other attendants. The grasses show what Stebbins (1974) called an extreme adaptation for wind-pollination and cross-fertilization: lodicules controlled by weather; elongation of the stamen filament leading to anthers being presented in a new orientation, pollen quickly shed into the air, abundant, light, easily dispersed; large easily exserted stigmata. Yet, none of these attributes prevents (i) a high level of compatibility between sibs where seed dispersal results in a very narrow distribution, (ii) the mutation self-incompatibility to self-compatibility, (iii) the evolution of the diverse floral array seen in the family.

Pandey (1977) even sees the pseudocompatibility and the high level of sib-compatibility that arise from the two-loci incompatibility system, as extremely advantageous in long-distance dispersal from a single diaspore; both these characters are usually interpreted as the least efficient aspects of the two-loci complementary system. The accidental arrival of a second diaspore from a long distance, and a second accident is as likely as the first, will restore the incompatibility system.

The reevolution of a self-incompatibility system from derived self-compatibility as described by Pandey (1977, 1980) is of very low likelihood if the taxa had long been self-compatible. Added to this, there is no known self-incompatibility system in the grasses that could have had a two-loci complementary system as its progenitor; if such a system were to evolve, it would be of the less efficient one-locus *Tradescantia* type. For those self-compatible grasses where an outbreeding system would be advantageous and which selection might favor, the choice is among various forms of monoecism and dioecism. The proposals of Charlesworth & Charlesworth (1978a, 1978b) for the evolution of these states demand the presence of high levels of self-compatibility; these proposals accord with the potentialities indicated by Pandey (1977, 1980).

CONCLUSION

Is there an optimal breeding system for the Gramineae? Self-incompatible hermaphrodite flowers in many-flowered spikelets, in inflorescences of many spikelets would seem a very efficient option; such a combination of characters would annually yield a large number of seeds of varied genotype, and no secondary characters would be involved. This state is reached in its fullest expression in the Festuceae, and in some related tribes in the Festucoideae, such as Aveneae, Bromeae, and Hordeeae. Such a conclusion is valid only within the narrow confines of the questions being examined. The conclusion makes no allowance for any other factors preceding seed setting, e.g., floral induction, or consequent upon seed setting, e.g., seed dispersal; it makes no allowance for any ecological considerations, e.g., duration of growing season; it makes no allowance for life-history, e.g., annuals or perennials. And it makes no allowance for the natural distribution of the tribes of grasses on the face of the earth.

The Festucoideae are not especially well known for alternative reproductive systems, self-compatibility excepted; apomixis is known in *Calamagrostis, Hierochloe, Poa,* and very slightly in *Agropyron*; there is very sparse dioecism, and little monoecism, much of it in *Poa.* Members of this subfamily show that, although apparently possessing many of the characters that would seem the most advantageous, other breeding systems have evolved if even only sporadically, or are now the residuum of evolution.

Any analysis leading to the conclusion favoring the festucoids as possessing the most efficient breeding system in the grasses could be a biased one, biased by the overwhelming evidence from temperate grasses. That so many grasses differ from the festucean model reflects the fact that the adaptive values for grasses include more than the requirement of a self-generating incompatibility system, and indicates that one seed in an andromonoecious spathate raceme, or monoecious axillary paniculodium, may well have equal or superior adaptive values in the tropics and subtropics.

The Gramineae, if viewed solely by the array of breeding systems found there, is an advanced family in the Monocotyledonae. Stebbins (1974) found that the grasses are ". . . the climax of flowering-plant evolution . . . ," but his conclusion was logically based on an examination of all the qualities in the family. Bews (1929) was astonished that such an unspecialized system of pollination could be associated with so successful a family.

The grasses show relative conservatism in the arrangement of the flower; in the development of the breeding systems associated with those flowers there is relatively less conservatism, though never flamboyance. The major reproductive systems known in the Plant Kingdom are represented except heterostyly, sporophytic control of incompatibility, and overt insect pollination, though entomophily probably occurs in the tropics.

Although there are some unexpected features of the incompatibility system (Lundqvist, 1954, et seq.), and some unique conditions at pollination (Heslop-Harrison, 1979, 1980), self-incompatibility is basic to the family. For an hermaphroditic, anemophilous, self-incompatible group, optional ways of ensuring seed setting are those leading towards (i) self-compatibility in demanding ecological conditions; (ii) production of abundant pollen to ensure cross-fertilization in competitive genetic conditions; (iii) espousal of apomixis in conditions of polyploidy, and of hybridism. Under self-compatibility as described in (i), initial significant inbreeding depression would be the major disadvantage; for the cross-pollination proposition an excess of flowers that are pollen producers only (andromonoecism) places a low genetic value on ovules and leads to their loss from flowers; and apomixis has always been selected against, resulting in the facultative rather than the obligate form.

There was an early and frequent loss of the incompatibility system without polyploidy as a direct cause, yet self-compatibility is an essential prerequisite only for the development of cleistogamy. Dioecism could evolve from self-compatible progenitors, as could monoecism. For self-compatible grasses an escape is dioecism; monoecism does not guarantee that surcease. Hermaphroditism, alone or in some monoecious combination, sustains most of the world's grasses, and those grasses that are the sustenance of the world.

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