



Brachiaria: Biology, Agronomy, and Improvement

Edited by: J. W. Miles, B. L. Maass, and
C. B. do Valle,

with the collaboration of
V. Kumble

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Cover photograph:

Brachiaria seed multiplication plot, Popayán, Cauca Department, Colombia.

Photo by Fernando Pino, CIAT.

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Chapter 8

Reproductive Physiology, Seed Production, and Seed Quality of *Brachiaria*

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Abstract

Seed of six commercial *Brachiaria* species is extensively produced for pasture sowing. Production is restricted geographically and seasonally by photoperiodic flowering reactions. It also requires a prior control of vegetative tiller production, and therefore a reliable dry season. The necessary conditions are most readily found at high tropical latitudes.

Seed crop management is mostly conventional. Vigorous synchronized tillering is stimulated by decapitation and use of nitrogenous fertilizer at times when rainfall, temperature, and sunshine are expected to favor unrestricted development. Ripe seed sheds readily and, coupled with imperfect synchronization of crop ripening, tends to make conventional direct harvesting inefficient and its timing critical. Where possible, seeds are let to fall and accumulate, and then recovered. Seed yields range from more than 1,000 kg/ha of pure seed to less than 100 kg/ha.

Seed quality is heavily influenced by vitality and dormancy. Vitality depends mostly on maturity of seed at harvest, being higher in accumulated fallen seed and much lower in directly severed seed. Dormancy is strongly developed in the genus and persists in most taxa at least

into the season after harvest. This creates problems for germination testing and in the field use of fresh seed. Breaching the husk, most commonly by sulfuric acid, provides a partial solution.

Suggestions are offered for improving seed production when developing new cultivars, particularly for selecting flowering control mechanisms compatible with production at low latitudes.

Introduction

Six taxa of *Brachiaria* are important enough as pasture plants to be grown extensively for seed—*B. decumbens*, *B. humidicola*, *B. brizantha*, *B. mutica*, *B. ruziziensis*, and *B. dictyoneura*¹ as demonstrated in this volume by Argel and Keller-Grein (Ch. 14), Pizarro et al. (Ch. 15), and Stür et al. (Ch. 17). In these chapters and that of Keller-Grein et al. (Ch. 2), the history of these materials is also described. Too little is known of other members of the genus to provide a coherent picture of their reproductive behavior.

Our objective here is to characterize the reproductive properties of the group and identify what may be needed in future cultivars. In this paper, we emphasize:

1. *Brachiaria decumbens*, derived from the Australian introduction CPI 1694 and equivalent to cv. Basilisk (Oram, 1990).

1. Unless otherwise indicated, references to *B. dictyoneura* are to accession CIAT 6133 = cv. Llanero.

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2. *Brachiaria humidicola* material derived from the Australian CPI 16707 and released as cv. Tully (Oram, 1990).
3. *Brachiaria brizantha*, the Brazilian cv. Marandu (Nunes et al., 1984), is distinct from other, now less important, early introductions, which include the Colombian cv. La Libertad (Ramírez P., 1987).
4. *Brachiaria mutica*, long naturalized in many countries and containing at least some variation (Wesley-Smith, 1973), but no specific cultivar.
5. *Brachiaria ruziziensis*, an apparently uniform type, formerly very widely distributed (Barnard, 1969; Serrão and Simão Neto, 1971; Stür et al., Ch. 17, this volume).
6. *Brachiaria dictyoneura*, introduced as CPI 59610 to, and widely evaluated by, CIAT, was released as cv. Llanero in Colombia (ICA, 1987).

Reproductive Physiology

All *Brachiaria* species may be propagated both vegetatively and from seed. Vegetative propagation is simple, but, except in very small-scale farming, impracticable. Here, we consider only reproduction from seed.

All taxa are derived from collections, each perhaps of single plants, made from wild populations, mainly in tropical eastern Africa. Because only the source of supply, and not the point of collection, is normally given in cultivar descriptions, our material cannot be readily related to a background of either local adaptation or original population diversity. Rationalizing reproductive behavior in terms of natural adaptation is therefore difficult.

The study of reproductive processes in *Brachiaria* has been influenced mostly by agronomic research needs to rationalize flowering behavior. Although

such research, from a physiological viewpoint, has been superficial, it has provided a working framework that can be used, with caution, until more complete information becomes available.

Inflorescence development

A young plant will not initially produce inflorescences; to explain this, some form of juvenility is usually inferred. An inflorescence population developing from a seedling sward is slow, sparse, poorly synchronized, and of little practical value. Reproductive development is therefore best viewed as starting with the proliferation of tillers in an established sward. In all taxa, this is stimulated both by the decapitation of existing tillers and by an abundance of available soil N. Such effects are widely observed in grasses, but still poorly understood (Murphy and Briske, 1992). Decapitation is effective, perhaps because apical dominance is removed and light penetrates better to bud sites. The two influences are exploited together to produce the dense population of similarly aged tillers, which, if subsequent conditions for growth and floral differentiation are favorable, will develop into the seed crop.

The conditions required for growth of tiller populations are ample, continuous supplies of freely available soil moisture, mean daily temperatures above 23 °C, high levels of solar radiation, and soil nutrients (especially N) in sufficient quantities for rapid pasture growth. Under such a combination of conditions, tiller populations rapidly grow to a density at which they inhibit further recruitment, thus producing a discrete burst of development—the basis of the relatively closely synchronized population of inflorescences that constitutes the conventional seed crop.

Flower initiation also has specific photoperiodic needs, which differ among species and restrict both the latitude and time of year at which vigorous flowering may occur. The fragmentary evidence available 10 years ago (Ison and Hopkinson, 1985) showed *B. mutica* to be

an obligate short-day plant, and *B. ruziziensis* to be a quantitative short-day plant, both flowering with enough vigor for useful seed production only after the autumnal equinox in the high tropics and subtropics. *Brachiaria decumbens*, *B. humidicola*, and *B. brizantha* were inferred to be quantitative long-day plants, flowering everywhere in the longer days of the year, and more vigorously at high than at low tropical latitudes. *Brachiaria dictyoneura* cv. Llanero has since been shown to behave similarly (CIAT, 1986; Diulgheroff et al., 1990; Vela et al., 1991; M. Sánchez, J. E. Ferguson, and A. Ortiz, unpublished data).

Flower initiation in individual tillers is sometimes inhibited even when daylength favors it. For example, apices of tillers of *B. humidicola* that emerge into an existing dense sward, either of vegetative tillers or of stubble, are apt to remain indefinitely vegetative. This makes it almost impossible to take more than one crop in a season, and even then difficult, unless the sward is razed. The same effect is apparent in other species to variable, although usually lesser, degrees, especially in climates where temperature and rainfall are such that vegetative growth continues unchecked throughout the year. Stür's analysis (1985) of seed crop development in *B. decumbens* suggests that, among other symptoms of competitive suppression, late-emerging tillers are slower than early ones of the same population to reach inflorescence exertion, and more likely to remain indefinitely vegetative (Stür and Humphreys, 1987). If tillers of the same population, emerging only 5 days apart, can interfere with one another's reproductive potential, then similar competitive forces may explain why much older and bigger tillers suppress emerging tillers.

Flower initiation is followed by inflorescence differentiation and emergence. Stür (1986) recorded the course of differentiation in *B. decumbens*, which is believed to be similar in major details to that in other species. The

initially vegetative shoot apex elongates, initiates racemes, and degenerates. The racemes develop "ridges," which differentiate into spikelets, which then differentiate into floral parts. The whole process is rapid. Floral initiation may occur within 6 days of tiller emergence, spikelet differentiation may start within 10 days of flower initiation, and first inflorescences may emerge about 4 weeks later (Stür and Humphreys, 1987).

The cessation of tiller emergence and the weaker development of late-emerging tillers brings the phase of inflorescence emergence to a close. It lasts a variable time—Stür (1985) recorded it as 28 days—and largely sets the pattern of spread over time of crop ripening. The density of emerged inflorescences is the main determinant of spikelet density; hence, of potential seed formation. Potential inflorescence density differs among taxa, being highest in *B. humidicola*, sometimes approaching 2,000/m²; intermediate in *B. decumbens*, *B. dictyoneura*, and *B. ruziziensis*, in which it commonly reaches 700-1,000/m²; and lowest, at about 200/m², in *B. brizantha* (Andrade et al., 1983; Stür, 1985; present authors, unpublished data).

Seed development

After inflorescence emergence anthesis of spikelets occurs. Anthesis on a single head, and between heads in a population, is staggered over time, although not enough to significantly affect the overall spread of crop ripening. Pollination is required, whether seeds develop sexually or apomictically (Valle and Savidan, Ch. 10, this volume). *Brachiaria ruziziensis* is sexual, the others are predominantly apomictic (Ferguson and Crowder, 1974; Pritchard, 1967; Valle, 1986; 1990). How dependent the success of seed set (the formation of a recognizable caryopsis) in the crop is on the influence of either apomixis or the genetic irregularities associated with polyploidy (Sotomayor-Rios et al., 1960) is, so far, impossible to assess. Also usually difficult is to equate caryopsis contents of

samples with success of pollination, because discrimination is seldom possible between preanthesis and failed-set spikelets in the empty fraction. Caryopsis contents rarely exceed 30% (Stür, 1985; F. H. D. de Souza and J. M. Hopkinson, unpublished data), and overall seed set of the heaviest yielding crops of, for example, *B. decumbens*, is unlikely to exceed 40%. But the importance of the various possible genetic causes of such failure remains open to conjecture.

Failure of seed set has other, more tangible, causes too, the commonest being drought stress in the crop at anthesis. This is conspicuous in *B. humidicola* in Australia in dry years, and is probably common in both *B. decumbens* and *B. humidicola* growing on sandy soils in Thailand (W. W. Stür, 1994, personal communication). Seed set of *B. humidicola* fails consistently in Colombia, despite prolific flowering and abundant moisture (J. E. Ferguson, 1994, personal communication). Similar failure was recorded in *B. brizantha*, *B. decumbens*, and *B. dictyoneura* at 6° 30' N in Antioquia, Colombia (Osorio et al., 1991). This kind of behavior raises the possibility of photoperiodic response varying with stage of development, for which precedents exist among other warm-climate grasses (Ison and Hopkinson, 1985).

Caryopsis development follows seed set. The caryopses of all *Brachiaria* species reach a finite size at maturity that varies only within narrow limits and is set by the dimensions of the husk, which remains remarkably constant within any taxon. In this respect, *Brachiaria* species are like other tight-husked panicoid grasses, contrasting with those whose caryopses, not being enclosed in rigid structures, can vary greatly in size at maturity (e.g., species of *Chloris* and *Cenchrus*, and many *Andropogoneae*).

The attainment of maturity, without which high seed vitality cannot exist, apparently depends largely on the rate of growth of the caryopsis, relative to the rate of development of the abscission

layer. In the similarly structured *Panicum maximum* seed, the time taken for the abscission layer to develop is relatively constant, whereas the time taken for the caryopsis to mature is variable and dependent on seasonal weather (Hopkinson and English, 1982c).

This conclusion may apply equally to *Brachiaria*. Cool weather or prolonged overcast periods, for example, retard caryopsis growth, with the risk that abscission will precede maturation in a high proportion of spikelets. This results in abnormally high proportions of immature seeds even at harvest ripeness, inevitably reflected in the condition of the harvested seed. Variation in immature seed content is a major cause of differences in seed quality between districts or seasons. An immature caryopsis, besides being itself incompletely developed, fails to occupy its husk cavity fully. Because the seal between the lemma and palea depends on their overlapping parts being forced together by the final growth of the caryopsis, and because the protective capability of the husk depends on a tight seal, a secondary effect of immaturity is defective protection against rapid entry of foreign bodies such as water or fungal hyphae. This leaves immature seed vulnerable to damage and disease, as well as physiologically weak.

The extent of maturity of a population of pure seeds is easily judged from a measure of the average pure-seed spikelet weight, the reliability of the figure being dependent on the uniformity of spikelet dimensions. In *B. decumbens* cv. Basilisk, for example, <450 mg/100 seeds indicates a low, 450-500 a moderate, and >500 mg/100 a high level of maturity. Mature seed weights for other taxa are about 650 mg/100 for *B. brizantha*; 500-650 for *B. ruziziensis*; 400 for *B. humidicola*; 110 for *B. mutica*; and variable in *B. dictyoneura* cv. Llanero, 480-550 being recorded under some conditions, 560-620 under others (Diulgheroff, 1991; Phaikaew et al., 1993; present authors, unpublished data).

Seed retention

Abscission is common to all commercial *Brachiaria* species. It occurs shortly after gross physical development (but not every detail of maturation) is complete, and thus results in brief peaks in the quantities of seed retained on the crop. Prolonging retention apparently does little to improve seed recovery efficiency. As the abscission layer is between the glumes and the pedicel, methods tried with other grasses to improve retention, such as spraying with adhesives or selecting plants with tightly enclosing glumes, offer little hope. Individuals or populations with faulty or delayed abscission have not been found so far.

All the events so far described influence the pattern of retention of ripe seed on the standing crop. This has been much measured, being central to harvest strategy, and is highly variable. Individual taxa, however, have characteristics recognizable through the mass of other variations. Seed ripening tends to be the most closely synchronized in *B. humidicola*; intermediate in *B. decumbens*, *B. dictyoneura*, and *B. ruziziensis*; and least in *B. brizantha* commercial cultivars.

Seed Production

The capacity to produce cheap, abundant, high-quality seed is crucial to the widespread adoption of a pasture cultivar. This has been demonstrated many times in the history of *Brachiaria*. For example, the value of *B. decumbens* was known in Queensland in the 1940s (Schofield, 1944), yet its adoption was delayed until the 1960s, when a combination of factors—realization of the existence of dormancy (Grof, 1968), discovery of suitable seed-growing districts, and use of combine harvesters—stimulated the first large-scale seed production. Similar trends of events have since been repeated in other species. A recent example is the adoption of cv. Llanero in Colombia,

resulting from successful local seed production, after the failure of seed production in otherwise useful species (ICA, 1987; M. Sánchez et al., unpublished data).

Local seed production is usually preferred, and is sometimes the only possible course, but importation is an option for many countries, and, as a result, a substantial world trade in seed has developed. The main exporters are Brazil (to other tropical American countries [Santos Filho, Ch. 9, this volume]) and Australia (to the western Pacific and Southeast Asia [Stür et al., Ch. 17, this volume]).

The original focus of seed production, in the early 1970s, was Australia, with *B. decumbens*. This helped set in motion the massive expansion that took place in Brazil a few years later and made Brazil by far the dominant producer. Since then, the choice of species has widened, and their use increased; many other countries now produce seed. Table 1 lists recent production records, although these may be incomplete because of a lack of information.

Success in seed production comprises four major elements: locality for growing the crop, crop management system, harvesting method, and attention to the problems of seed quality. Of these, the first is of overriding importance: if this choice can be correctly made, then the complications of the others are greatly reduced. Harvesting method, although influenced by the first two, is essentially governed by economic rather than biological factors, particularly by the relative availability of capital and labor.

Choosing a locality for seed production

There is economic incentive to produce seed wherever a pasture or fodder crop sward is successful. Geographical limits to pastoral use are discussed in other contributions to this volume (Fisher and Kerridge, Ch. 3; Keller-Grein et al.,

Table 1. Estimates of recent annual seed production of commercial *Brachiaria* species.*

Region or country	Seed production (t/year) ^b					
	bri	dec	dic	hum	mut	ruz
Australia	0	150	0	50	2	0
Tropical America						
Bolivia	10-20	10-20				
Brazil	40,000	40,000		>500		100-400
Central America and Mexico	5-10	5-10	5-10			
Colombia		20-50	10-20			
Cuba		10-20				
Peru		10-20				
Venezuela	50	50		50-100		
Asia						
India						40
Thailand						450-630

a. Gaps denote lack of information.

b. Species: bri = *B. brizantha*; dec = *B. decumbens*; dic = *B. dictyoneura*; hum = *B. humidicola*; mut = *B. mutica*; ruz = *B. ruziziensis*.

SOURCES: Tropical America, excluding Brazil: CIAT, 1990; Brazil: F. H. D. de Souza, estimated data; India: Kerala Livestock Development Corporation, unpublished records; Thailand: Phaikaew et al., 1993; Phaikaew and Pholsen, 1993; Australia: J. M. Hopkinson, estimated data.

Ch. 2). They are set climatically, primarily by limits of adaptability to low temperatures and low rainfall, and, in the Americas, by the severity of spittlebug predation. Within these limits are environmental requirements specific to seed production.

The first requirement is to match conditions that favor unrestricted crop growth with daylengths that satisfy photoperiodic needs for vigorous flowering. This applies to all taxa equally, their specific and differing requirements being largely a reflection of their different photoperiodic responses.

Within any one country and for any one taxon, achieving this match depends on the range of latitudes and climates available. It is most readily met for long-day taxa when they are grown as summer crops at high tropical latitudes in districts with a reliable summer wet season, while the short-day plants in the same places depend on the continuation of both rainfall and warm temperatures into the tropical "winter."

The greatest difficulties arise at low latitudes, where the period of long days is

too short to promote vigorous flowering in long-day taxa. A clear example comes from Colombia, where at about 5° N, *B. humidicola* flowers but fails to set seed, and seed production of *B. decumbens* and *B. brizantha* is very low. Only *B. dictyoneura* cv. Llanero flowers and sets seed vigorously enough to permit commercial seed production, which has been of critical importance to its adoption there (Sánchez and Ferguson, 1992). Improvement of seed production with increasing latitude is difficult to judge with accuracy, because of the influence of confounding factors, such as low soil fertility. In Peru, at 6-8° S, for example, yields of long-day taxa are low, possibly for other reasons (Vela et al., 1991). Their potential is undoubtedly better at 10° N, judging by the successes in Costa Rica (Diulgheroff et al., 1990; Sylvester-Bradley and Ferguson, 1993).

The second requirement, which applies particularly to the long-day taxa, is to prevent the inhibition of flowering by a continuously dense vegetative sward (see p. 125-126). This is most easily achieved under conditions where drought curtails vegetative growth. Drought also

appears to improve subsequent synchrony of tiller growth, presumably both by reducing sward density and by allowing soil N to accumulate, leading to its later sudden release in abundance when the drought breaks. Hence, a distinct, reliable dry season immediately before the main seed cropping period would be useful.

Suitable combinations of photoperiod and rainfall distribution occur between about the tenth parallel and the Tropic in either hemisphere, and the most successful seed-growing regions are located in these regions.

Once these two needs are satisfied, other specific climatic details can be taken into account. Although production is possible under a wide range of conditions, it is efficient only in part of that range. Relevant factors are mostly local, such as the risk of loss from prolonged wet weather at harvest. But, if seed production is to be commercially viable, the seed function must combine with other uses, such as grazing, hay, and rotation, which make other demands on the plant and emphasize its need to be well adapted to soil conditions and climate. Because the optimal combination of all factors is different for each taxon, a geographical mosaic of suitability tends to occur, in which different districts favor different seed crops. Even this may change with time as patterns of factors change and demand fluctuates.

Market forces tend eventually to reduce seed prices to levels that eliminate production in less-favored districts. This happened, notably, in Queensland in the 1970s, when *B. decumbens* seed production boomed as both domestic and export markets grew, and led to sowings under a very wide range of conditions. It resulted in a shift of production from tropical (18° S), high-rainfall (3,000 mm) districts on the coast to adjacent drier (1,300 mm), upland areas in which yield and seed quality were greatly improved. Thus, sale prices fell to levels that were

uneconomic in the less productive districts. Similar effects also dictate the pattern of seed production in the vastly more extensive and less abruptly variable region of central Brazil where seed is grown. There, most seed is produced in northern São Paulo state, in two relatively restricted localities: Auriflama, which favors *B. brizantha* cv. Marandu, and Brodosqui for *B. decumbens* cv. Basilisk.

Those countries that need seed but have no suitable seed-growing districts usually lie at low latitudes or are island states too small for much climatic variation. Their choices, then, are to import seed, seek alternative grasses, or accept low, unreliable seed yields.

Crop management

Most seed production of *Brachiaria* is purposeful, as distinct from opportunistic, as it is with many extensively grown grasses. The exception is *B. mutica*, which commonly grows on land too wet to be reliably harvested and where preharvest management is likely to be wasted. Even this taxon, however, responds to planned management when this is possible.

Once the match with the environment is obtained, seed crop management becomes a matter of aiming for the development of the highest density of seed heads in as close a synchrony as possible. This is done by the long-established method of cutting back the sward and applying nitrogenous fertilizer (see p. 125).

The need for synchronization of seed ripening depends on the harvesting method. If harvesting is done by a single act of severing the seed from the plant, then synchronization is important. If, however, harvesting is done by repeatedly collecting shaken-off seed (Phaikaew et al., 1993) or of accumulated fallen seed, synchronization is less important. Even with the first method, improving synchronization is not necessarily desirable beyond a certain point. Spread over ripening time, while reducing the maximum yield potential, provides some

insurance against misfortune at peak ripeness and some flexibility in the management of large areas of crop. *Brachiaria humidicola*, in particular, is already tightly synchronized under conventional management, often allowing for no more than 3 days for mechanized harvesting before too high a proportion of the crop is shed. The next most closely synchronized are, in order, *B. dictyoneura* (Diulgheroff, 1991), *B. ruziziensis* (Kowithayakorn and Phaikaew, 1993), and *B. decumbens*. Although they are less vulnerable, 50% of their standing pure seed is apt to fall within a week of peak production. *Brachiaria brizantha* cv. Marandu is so poorly synchronized that a single cut of the standing crop will yield only about 10% of the potential, and even that is of poor quality.

The competitive vigor of *Brachiaria* species generally prevents weeds from invading, except during establishment. Even so, *Brachiaria*'s remarkable tolerance of the herbicide atrazine makes most weed control possible (Hawton, 1980). Diseases and pests present few problems specific to seed crops (Valério et al., Ch. 6, this volume). In Australia, a fungal disease—a false smut, *Ephelis* sp. (J. L. Alcorn and R. D. Davis, 1994, personal communication)—reduces seed yield of *B. humidicola*. In Brazil, an ergot, *Claviceps sulcata* (Fernandes et al., 1992), reduces both yield and—through its sticky exudate—efficiency of recovery of *B. decumbens*, especially in late crops. Its extent and severity is such as to warrant investigation of control strategies. Throughout the American tropics, spittlebugs may affect seed crops, especially those of *B. decumbens*, although the pest's significance is as yet unmeasured. A native field rat occasionally causes massive crop losses in Australia, severing the inflorescences to get at the seeds.

Recognition of ripeness

For those crops whose seed must be severed, much attention has been paid in the literature to recognition of ripeness and to the usefulness of measurable

characters for identifying the point of maximum seed retention to determine optimal harvest time (Condé and Garcia, 1983; Gonçalves et al., 1980; González, 1987; Kowithayakorn and Phaikaew, 1993; Oliveira and Mastrocola, 1980). Such literature educates the reader in the dynamics of crop development, but tends not to produce commercially useful criteria. Crops are too variable and the factors too numerous for rule-of-thumb methods to be appropriate. Decisions continue to depend on intuitive integration of these factors through experience, observation, and an understanding of the variable dynamics of the system. However, such decisions become irrelevant when shed seed is to be harvested.

Harvest

Many harvesting methods are used, each matched to the economics and balance of labor to capital of the farming system in which it is used. In small-scale systems, with cheap manual labor, seed may be repeatedly shaken from the heads 'by hand, or heads may be tied into "living sheaves" for seed to accumulate, or the heads may be hand-cut and "sweated" to loosen the seed before separation (Kowithayakorn and Phaikaew, 1993). In large-scale systems, with cheap labor and a reliable dry season, as in parts of Brazil, seed of *B. decumbens* and *B. brizantha* is allowed to fall and accumulate on the ground, from which it is later swept up by hand (Souza, 1991; Santos Filho, Ch. 9, this volume).

For intermediate levels of production scale and mechanization, tractor-mounted beater systems have been designed (Ramos, 1991), which selectively recover mature seed, although at a relatively low proportion overall (30%-40%) of the standing crop (Cardozo et al., 1991). In capital-rich systems, such as in Australia, crops are either combine-harvested, with the attached standing seed being taken conventionally as if it were a grain crop (*B. humidicola* and formerly *B. decumbens*), or the seed is allowed to fall and accumulate on the leaf mat of a

heavily fertilized sward before being gathered with the cutter bar close to the ground (*B. decumbens*) (Hopkinson and English, 1982b). The development of this method and the yield increases it brought are detailed by Hopkinson and Clifford (1993).

Harvest efficiency, an important issue with many seed crops, has received little attention with *Brachiaria*. It acquires most significance in crops in which the standing seed is direct-combined, that is, primarily *B. humidicola* in Brazil and Australia, and, to a lesser extent, other species in both countries and Colombia. Records of harvest efficiency in such crops are sparse. Hopkinson and English (1982a) recovered, on the average, more than 80% of standing seed of *B. decumbens*, although only about 30% of total seed present. Cardozo et al. (1991) combine-harvested an average of almost 50% of what was available for hand harvesting in *B. dictyoneura* cv. Llanero crops.

Seed processing

All seed recovered directly from the crop must be dried after harvest because moisture contents can be as high as 60%, and the usual target for storage is about 10%. Rapid drying can be harmful, apparently because final maturation continues after severance (Hopkinson et al., 1988). Many methods of drying are used, from simple sun-drying on hard surfaces to bin-drying with forced drafts of warmed air.

Undried seed is, metabolically, still highly active, and if packed tightly in bulk, as with all combine-harvested seed, may be unable to dissipate heat and waste gases generated by metabolism. Accumulation of either or both is rapidly fatal to seed. Measures must therefore be taken to ventilate such bulks if drying is delayed, and failure to do so is a frequent cause of lowered quality.

Provided suitable facilities exist, drying, cleaning, and storage present few technical problems. That is, difficulties

usually stem from deficiencies in available technology rather than from any peculiarities of the plant. Drying and safe storage under wet tropical conditions is difficult for small farmers without capital. In Brazil, the combination of mechanized harvesting of large areas of *B. humidicola* with open-air drying and casual bulk handling of seed leads to much deterioration. This has given the crop an otherwise undeserved reputation for low seed quality.

Seed yields

Yields of pure seed are highly variable, and have meaning only within their specific context of locality, management system, and harvesting method. As tropical pasture grasses, all *Brachiaria* taxa are potentially high-yielding, but most crops fall well short of their potential. Restrictions on choice of environment and management options, harvest inefficiency, and unreliable weather are the main contributors to the shortfall.

Brachiaria decumbens in Queensland occasionally reaches 1,000 kg/ha of pure seed when accumulated fallen seed is combine-harvested under optimal conditions, but the commonest range for a specialist would be 300-800 kg/ha per crop, with one, sometimes two, crops per season. A standing crop conventionally combine-harvested seldom exceeds 300 kg/ha per crop. Expected yields of swept-up crops of *B. decumbens* and *B. brizantha* in Brazil are about 1,000 kg/ha; those of combine-harvested crops, much lower. Hand-cut and sweated crops of *B. decumbens* in Costa Rica yield 70-150 kg/ha of pure seed, and of *B. brizantha* 60-90 kg/ha, while at lower latitudes, as in Colombia, both species tend to produce considerably less (present authors, unpublished data).

Brachiaria humidicola in Australia occasionally exceeds 400 kg/ha of pure seed with direct combine-harvesting, but records of 20 closely monitored crops gave an average of only 140 kg/ha for harvested

crops and a 30% risk of no harvest, figures that reflect the great risk of loss with this crop (B. H. English and J. M. Hopkinson, unpublished data). Rayman (1981), referring to extensive harvesting in Brazil, quoted 80 kg/ha of seed as an average. In Costa Rica, 50-160 kg/ha is the usual range (S. Diulgheroff, unpublished data).

Yields of *B. ruziziensis* from northeast Thailand are quoted as 300-500 kg/ha of high-quality seed harvested by the "living sheaf" method; and 150-250 kg/ha by cutting and sweating (Phaikaew and Pholsen, 1993; Phaikaew et al., 1993). Few useful figures exist on yields of *B. mutica*. A token 20 kg/ha of saleable seed is expected from unmanaged combine-harvested crops in Australia, but a much greater potential clearly exists.

For Costa Rica, Sylvester-Bradley and Ferguson (1993) report 230 kg/ha of cleaned seed of cv. Llanero in one season, while others quote a range of 120-425 kg/ha (Diulgheroff et al., 1990; Pizarro et al., 1989). A report of 120 kg/ha comes from Ecuador. Numerous records from Colombia exist, with recent, commercial, combine-harvested averages of about 27 kg/ha pure seed, with the best single crop yielding 122 kg (Sánchez and Ferguson, 1992). In a comprehensive series of trials over several seasons and sites, Cardozo et al. (1991) averaged 87 kg/ha pure seed with hand harvests and 48 kg with a combine harvester.

Seed Quality

Conventionally, seed quality has three components: genetic, physical, and vital. Technically, high standards of genetic and physical quality in *Brachiaria* seed are relatively easy to maintain. Vital quality, however, is beset with technical pitfalls that require detailed attention.

Vital quality has two sides: vitality of the seed, that is, its vigor and viability, and the unrelated property of dormancy, which affects planting value and complicates the measurement of vitality.

Vitality

High levels of vitality can be attained only if the seed has the opportunity to mature thoroughly. It thus depends on both the environment for crop growth and on the harvesting method. Immaturity through premature abscission, as earlier described, is common only when the environment is faulty, that is, when the crop is grown at the wrong time of year, in the wrong place, or in a difficult year. Thus, immaturity is only an occasional issue in successfully established seed-growing areas. Its occurrence otherwise suggests the need for close scrutiny of the crop's environment. A certain level of immature seed, often about 30%, is an inevitable component of seed harvested by severance—a consequence of the imperfect synchronization of ripening—whereas fallen seed is predominantly fully mature. This is one reason why swept-up seed is of better general quality than direct-combined seed in Brazil, and why most seed of *B. decumbens* is of higher initial quality than seed of *B. humidicola*.

The retention of vitality, as distinct from its attainment, depends first on preventing damage (whether by pests, diseases, threshing, overheating, suffocation, or rapid drying after harvest) and then on minimizing deterioration during storage.

Mechanical damage by threshing is severe only in crops that have to be threshed vigorously to detach the seed. Combine-harvested *B. humidicola*, in particular, suffers from this kind of damage. As a result, its seed tends to have a reduced dormancy but a shortened storage life. Other forms of damage reflect mostly inexperience, diminishing as industrial sophistication grows.

Deterioration with time is universal. *Brachiaria* seeds are orthodox: their rates of deterioration rise with increase in storage temperature and moisture content (Roberts, 1986). They therefore behave like other similarly structured seeds, and the equation derived to quantify the

course of deterioration in barley seeds in relation to temperature and moisture (Ellis and Roberts, 1981) provides at least an interim working prediction of deterioration in *Brachiaria* seeds.

Because they are grown, used, and stored in warm, humid climates and because they readily regain moisture from the atmosphere, *Brachiaria* seeds are prone to rapid storage deterioration. Measures can be taken, however, to mitigate this. While details depend on the practicalities of a given system, attention must first be paid to moisture content, even before temperature, as it is the more critical of the two variables over the normal range of variation, and the cheaper to control. Moisture content is especially important with seed cut directly from the plant, and of least concern with seed swept up in the dry season; such seed may be taken from the field with as little as 5% moisture.

Dormancy

Seed dormancy occurs in all groups of domesticated tropical pasture grasses, but is most conspicuous in those closely related genera of the Paniceae—including *Brachiaria*—whose caryopses are enclosed within a hard, tight husk. The husk, formed by the overlapping lemma and palea of the fertile floret, itself contributes to dormancy. Both husk and dormancy are particularly strongly developed in *Brachiaria*.

Dormancy has an obvious value for seed survival in the savanna ecosystems where most of these plants originated. Under domestication, it is both useful and troublesome. In seed production, it prevents germination in seed of *B. brizantha* and *B. decumbens* in the often-long interval between shedding and harvest. In sward establishment, it may delay emergence and even cause failure if the seed is too fresh when sown; however, it also serves to stagger germination over time, thus reducing risks of total failure under conditions of erratic rainfall. In seed testing, it is an unmitigated nuisance.

Normally all mature, undamaged seed is deeply dormant when newly harvested. As time passes, an increasing proportion of seeds lose their dormancy or become amenable to dormancy-breaking treatments. But also as time passes, the same seed ages: individuals die and survivors lose vigor at rates that vary with storage conditions (Ellis, 1988). The course of dormancy loss also varies, but in ways that are not yet understood. Percentage of germination tends to rise with time to a peak as dormancy weakens, then falls progressively as aging takes increasing effect. While the pattern is general, the timing of events and magnitude of the peak are widely variable. Under conventional storage and testing, the peak may be reached within a few months up to several years after harvest.

Dormancy in *Brachiaria* is imposed physically by the seed coverings and physiologically by embryo dormancy. The former is overcome in testing by removing, or sometimes merely by breaching, the husk (Renard and Capelle, 1976; Whiteman and Mendra, 1982). Acid scarification is the commonest method of breaching the husk, both in routine testing and in treatments for sowing (Castiblanco and Mendoza, 1985; Diulgheroff, 1991; Grof, 1968; ISTA, 1985; Macedo et al., 1994; McLean and Grof, 1968; Magalhães and Groth, 1992). Embryo dormancy presents greater difficulties. It diminishes progressively with age, and, although occasionally absent from fresh seed (Whiteman and Mendra, 1982), it typically inhibits germination in the early months after harvest. Numerous treatments may partially overcome it in testing. They include imbibing seed in potassium nitrate solution and exposing it to, for example, a range of oxidizing agents or plant hormones, temperature fluctuations, light of certain qualities, and dry heat (Atalla and Tosello, 1979; Castiblanco and Mendoza, 1985; Diulgheroff, 1991; Ellis et al., 1986; Goedert and Roberts, 1986; Oliveira and Mastrocola, 1983; Ortiz de

Acosta, 1984; Rodrigues, 1983; CIAT Seed Biology Section, unpublished data).

The significance of dormancy differs with species and circumstances. It is more of a problem in seed testing than in field establishment. It is of little concern with *B. mutica* and *B. ruziziensis*, and, apart from rare exceptions, is short-lived in *B. humidicola* (Atalla and Tosello, 1979; Macedo et al., 1994; Magalhães and Groth, 1992; Oliveira and Mastrocola, 1983). For *B. decumbens*, the tetrazolium viability test permits bypassing the dormancy problem during quality assessment of fresh seed. Of all species, *B. dictyoneura* cv. Llanero shows the most intransigence, with embryo dormancy lasting for as long as 2 years, and husk dormancy making acid scarification, necessary even for field use (Sylvester-Bradley and Ferguson, 1993). Both acid treatment and potassium nitrate are recommended for germination testing, but are only partially effective, except after very long periods of storage (Diulgheroff, 1991).

Except for *B. dictyoneura* cv. Llanero, dormancy is now seldom an issue for field establishment, probably because most farmers know to avoid using fresh seed for sowing. In Australia, acid treatment of *B. decumbens* was abandoned many years ago after it was shown to have no consistent benefit (Hopkinson, 1993). It was never used with *B. humidicola*, which is threshed so hard at harvest that husk damage substitutes for acid scarification. In Brazil, acid treatment to hasten establishment is restricted to *B. humidicola*, although most export seed of any species is still treated to meet quarantine requirements of importing countries. Brazilian farmers mostly use the sweeping-up method of harvesting for *B. brizantha* and *B. decumbens*. Such seed has weathered from lying in leaf litter, losing dormancy in the process, and thus making treatment unnecessary. In *B. mutica*, dormancy does not hinder the emergence of even relatively fresh seed (McLean and Grof, 1968), and, in

Australia, dormant seed is never acid treated. *Brachiaria ruziziensis*, likewise, is sown untreated in most countries where it is used.

Conclusions

Availability of abundant, cheap, high-quality seed is necessary, and will continue to be necessary, to support widespread use of current and future *Brachiaria* cultivars. Despite international trade in seed, local production will remain the preferred option. Hence, potential cultivars should be evaluated for their seeding capacity, as well as their usefulness as pasture plants, in the same geographical area.

The most striking aspects of *Brachiaria* seed production are the geographical variation in which success occurs, and the fact that seed production of a species may fail where it is valued as a pasture plant, especially at low latitudes. Photoperiodic flowering reactions seem to be largely responsible for this situation. If, in the development of new cultivars for specific regions, photoperiodic compatibility could be ensured, problems in seed supply may be greatly reduced. Ecotypic variation in photoperiodic response is common in grasses with a wide natural distribution (Foster, 1962; Tothill, 1966). It probably occurs in *Brachiaria* species too. If so, it may be possible to select or even breed for appropriate reproductive behavior during new cultivar development. The chief problem may be to reconcile improved seeding with high pasture quality, the two being, to some extent, mutually exclusive.

Another area of research is the inhibition of flowering by existing tillers, not only in *Brachiaria*, but also in the many other grasses in which it occurs. However, answers are likely to be both slow—it is a problem that has puzzled plant scientists since early days (Murphy and Briske, 1992)—and academic, without providing solutions to agronomic problems.

Within suitable environments, *Brachiaria* species are remarkable for their

success as seed crops. In the absence of market distortions, their seed is accordingly cheap. Shortfalls in supply occur, but seldom because of deficiencies in the plant. The incentive to look for fundamental improvements in seeding properties of the heavier yielders is weak. For example, a simple analysis of production costs of *B. decumbens* in Australia shows that improvement through increased seed yield beyond 1,000 kg/ha is not cost-effective, because the cost reductions that derive from greater yields are too small, relative to the fixed costs per kg of seed produced.

An improvement sometimes suggested is to prolong retention of ripe seed on the standing crop. Although the need for it has been circumvented in some species and under some circumstances, the genetic manipulation of abscission may be particularly useful for *B. humidicola*. Genetic variation in the extent of separation after formation of an abscission layer has been found in *Panicum coloratum* (Young, 1986), but, apart from some grain crops domesticated in ancient times, no tropical grass has been bred or selected for greater seed retention. If one were bred, care would be needed to ensure that increased retention does not become an ecological defect of the plant in the pasture.

The universally low percentage of seed set in *Brachiaria* may have genetic origins associated with polyploidy, or it may equally reflect a physiological limitation in, for example, the capacity to divert assimilate into reproductive activity. Causes of failure thus need to be understood before tackling low seed set.

Seed dormancy is a strong generic characteristic, inconvenient in seed testing and sometimes prejudicial to establishment. Its value for pasture persistence is often inferred, but is essentially unknown. Selection for weaker dormancy may be possible, but its consequences would be unpredictable. A safer policy would therefore be to persevere with understanding and

accommodating to dormancy rather than to change it.

To improve seed production of existing commercial taxa and develop production systems for new cultivars, researchers should involve, from the earliest stages, those who grow and know the seed crops, the producers and agronomists, whose initiatives over the last 30 years have contributed substantially to the remarkable success of the genus.

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References

To save space, the following acronyms are used in place of publishers' names:

- ASAP-Qld. = Australian Society of Animal Production, Queensland Branch
- CPAC = Centro de Pesquisa Agropecuária dos Cerrados
- CSIRO = Commonwealth Scientific and Industrial Research Organisation
- ICA = Instituto Colombiano Agropecuario
- INRA = Institut national de la recherche agronomique
- IPEAN = Instituto de Pesquisa Agropecuária do Norte
- NZGA = New Zealand Grassland Association
- NZIAS = New Zealand Institute of Animal Science
- NZSAP = New Zealand Society of Animal Production

- TGSA = Tropical Grasslands Society of Australia
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