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Flowering phenology, dispersal unit and germination in eight tropical perennial grasses

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Abstract: Phenological variation, seed yielding components, dispersal unit, seed setting and seed germination characteristics were investigated during monsoon growth (1995 and 1996) in eight tropical perennial grasses belonging to tribe *Andropogoneae*. *Vetiveria zizanioides* flowered after about 45 days of vegetative growth during mid-August. *Andropogon gayanus* was last to start inflorescence exsertion during second week of November, under strong short day condition, after > 4 months vegetative growth. Dispersal units are borne in apical and axillary heads. They are shed as diads, comprising two spikelets. Caryopsis accounted 15-48% of total dispersal unit weight. Weight of husk and appendages exceeded weight of caryopsis, awn accounted >60% of dispersal unit weight in *Heteropogon*, pedicelled spikelet contributed about 30% in *A. gayanus, S. nervosum* and *C. fulvus*. Seed setting varied from 21-75%. Germination in spikelets ranged from 12-56%, while germination in caryopses varied between 78 and 96%, except in *Heteropogon*. Freshly collected spikelets exhibited 3-6 months dormancy.

Resumen: Se investigaron la variación fenológica, componentes de la productividad de semillas, unidad de dispersión, el almacenaje de las semillas y características de la germinación de las semillas, durante la estación de crecimiento en el monzón (1995 y 1996) en ocho pastos perennes tropicales pertenecientes a la tribu Andropogonaceae. *Vetiveria zizanioides* floreció después de 45 días de crecimiento vegetativo durante mediados de agosto. *Andropogon gayanus* fue la última en empezar a producir inflorescencias durante la segunda semana de noviembre, bajo fuertes condiciones en días cortos, después de más de cuatro meses de crecimiento vegetativo. Las unidades de dispersión na cieron en cabezas apicales y axilares. Se des prendieron como diadas, comprendiendo dos espigas. La cariopsis sumó del 15 al 48% del total del peso de la unidad de dispersión. El peso de la vaina y de los añadidos excedió el peso de la cariopsis, la cual sumó 60% del peso de la unidad de dispersión en *Heteropogon*, las espigas pediceladas contribuyeron con cerca del 30% *en A. Gayanus, S. nervosum y C. Fulvus*. El almacenaje de las semillas varió del 21 al 75%. La germinación en las espigas varió de 12 a 56%, mientras que la germinación en la cariopsis varió entre 78 y 96%, excepto en *Heteropogon*. Las espigas frescas colectadas tuvieron una latencia de entre 3 y 6 meses.

Resumo: A Variação fenológica e as características das componentes da produção, da dispersão, formação e germinação das sementes de oito espécies herbáceas perenes tropicais do tribo das Andropogoneae, foram investigadas durante a estação de crescimento na monção (1995 e 1996). A *Vetiveria zizanioides* floresceu depois de 45 dias de crescimento vegetativo durante metade de Agosto. A *Andropogon gayanus* foi a última a iniciar a emergência da inflorescência durante a segunda semana de Novembro sob um regime bem marcado de dias curtos e depois de mais de 4 meses de crescimento vegetativo. As unidades de dispersão desenvolveram-se numa posição apical e axilar nas inflorescências. Elas apresentam-se geminadas compreendendo duas espiguetas. As cariopsis representaram 15-48% do peso total da unidade de dispersão. O peso da casca e aristas excederam o peso da cariopsis e representaram 60% do peso da unidade de dispersão na *Heteropogon*, com as espiguetas pediceladas a contribuírem com cerca de 30% na *A. gayanus, S. nervosum* e *C. fulvus*. A formação da semente variou de 21 -75%. A germinação nas espiguetas variou entre os 12-56%, enquanto que a germinação nas carriopsis variaram entre os 78 e os 96%, excepto na *Heteropogon*. As espiguetas colhidas frescas apresentaram dormência que variou entre os 3 e os 6 meses.

Key words: Caryopsis, diaspore, flowering phenology, inflorescence exsertion, resource allocation in diaspore, seed germination, seed setting, tropical grasses.

Introduction

Perennial grasses are major components of tropical pastures providing bulk of herbage for animals. Their flowering phenology, seed yield, purity (seed set in spikelets), and germination and dormancy are site specific characteristics which are influenced by latitude, altitude, and climatic conditions of the area (Crowder & Chheda 1982; Humphreys & Riveros 1986; Simpson 1990). The dispersal unit in grasses is a spikelet or a group of spikelets. In tribe *Andropogoneae,* the spikelets are born in pairs (diaspore); one spikelet (sessile) is hermaphrodite and may possess a caryopsis (depending upon seed setting) while the other spikelet (pedicelled) of the diaspore is staminate and sterile. In majority of cases, dispersal unit (diads or diaspore) are detached from the branches of panicles as a result of fracture below the glumes and the spikelet, with grains enclosed in glumes, are dispersed along with the pedicelled spikelets. However, while stripping the spikelet from panicles (during seed collection), the sterile spikelets are some time detached from the sessile spikelet with a stalk of sterile spikelet attached to it. In tropical grasses, a considerable portion of diads often remain empty due to low seed setting resulting into poor germination (Crowder & Chheda 1982; Boonman 1993).

Andropogon gayanus kunth, *Sehima nervosum* (Willd) Stapf., *Heteropogon contortus* (L.) Beauv.ex.Roem. and Schult, *Bothriochloa pertusa* (L.) A. Camus, *Bothriochloa intermedia* (R.Br.) A. Camus, *Chrysopogon fulvus* (Spring) Chiov., *Vetiveria zizanioides* (L.) Nash. and *Dichanthium annulatum* (Forssk) Stapf. are widely distributed in the tropical and sub-tropical regions of Asia and Africa. *S. nervosum* and *D. annulatum* are major components of *Sehima-Dichanthium* grass cover of India, while *Bothriochloa* spp., *C. fulvus* and *H. contortus* are found as an associate of this grass cover, and *Vetiveria zizanioides* is a major component *Phragmitis-Saccharum* grass cover of India (Dabadghao & Shankarnarayan 1973). *Andropogon gayanus,* a native to tropical Africa, was introduced as a fodder grass in India. All species are esteemed fodder except *V. zizanioides*, which play an important role in soil conservation (NRC 1993).

Studies on these eight range grasses were conducted to examine (i) the time of initial head emergence (IHE) and peak inflorescence density period after the commencement of monsoon initiated growth during June end, (ii) fertile tiller (tiller with panicles) characteristics, (iii) diaspore characteristics and resource allocation in diaspore, and (iv) dormancy and germination characteristics.

Materials and methods

The experimental site is located in the Central Research Farm of the Indian Grassland and Fodder Research Institute, Jhansi, India (latitude 25° 31′ longitude 78° 32′ E and altitude 237 m above msl). The soil was a sandy loam and slightly alkaline (pH 7.3) with 0.36% organic carbon, available N 167 kg/ha, P 9.2 kg/ha and K 193.3 kg/ha. Rainfall and temperature during growth, flowering and seeding is shown in Fig. 1. Rainy season received >90% of annual rainfall. Peak maximum and minimum temperatures recorded were : 47°C (June 2, 1995), 46.3°C (June 5, 1996), 1.8°C (January 30, 1995) and 0.8°C (December 11, 1996). Maximum soil temperature, 56 and 57°C was recorded during May and June.

Studies were conducted on 2-3 year old established pasture of each species during 1995 and 1996. The sward growth was monitored regularly after the start of monsoon rain in June end. The time of initial head emergence (IHE) was recorded for all species, when inflorescence exsertion started and about 10 heads /m² had emerged. The time of peak inflorescence density (which coincided with the com-

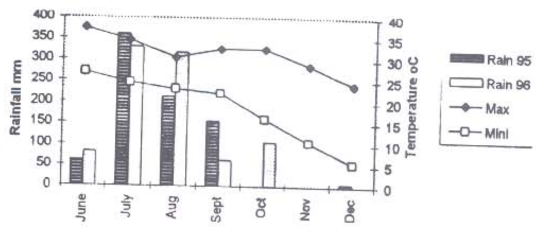

Fig. 1. Rainfall and monthly mean temperature (average of two years) of the site.

mencement of 'seed' shedding) was also noticed for all species. The time of IHE and peak inflorescence density period varied from mid-August to mid-December from species to species (Table 1). Length and diameter of fertile tiller, panicle length and diads/panicle were measured (Table 2) in randomly selected 25 tillers from three quadrats of one m^2 each (25 x 3). Seeds were also collected from the rest of the field when shedding was on the way and stored in polyethylene bags at room temperature. Observations on length and breadth of spikelets etc. were also recoded (Table 3). Weight of air dried pedicelled spikelets, caryopses, husk of caryopses and awn of fertile spikelets (1000 nos.) was recorded during 1995. Seed setting was determined by dehusking 500 sessile spikelets (100 x 5). Germination studies were conducted using sessile spikelets and seeds (caryopsis), obtained by dehusking

Table 1. Flowering phenology of perennial grasses.

Species	Initial Head Emergence (IHE)	Day length during IHE (h)	Temperature* during IHE°C	Period of peak inflorescence density
V. zizanioides	mid-August	13.00	32/24	September 2nd week
S. nervosum	Sept. Ist week	12.30	31/21	mid - September
H. contortus	Sept. 2nd week	12.25	32/23	October 1st week
B. pertusa	Sept. 3rd week	12.05	33/23	October 2nd week
D. annulatum	Sept. 4th week	12.00	35/21	mid - October
B. intermedia	Oct. 2nd week	11.40	33/19	November 2nd week
C. fulvus	Oct. 2nd week	11.40	33/19	mid - November
A. gayanus	Nov. 2nd week	10.55	29/12	December 3rd week

* Mean weekly maximum and minimum temperature (average of 1995 and 1996).

Table 2. Seed yielding components of perennial grasses.

Species	Fertile tiller ht. (m)	Diameter of tiller (mm)	Heads per tiller	Raceme per head	Panicle length (cm)	Diads per head	Diads per tiller
V. zizanioides	2.15 ± 0.2	4.8 ± 0.2	1	–	33.0 ± 4	1067	1067
S. nervosum	1.72 ± 0.1	1.6 ± 0.1	1	–	19.5 ± 1.6	35.8	35.8
H. contortus	1.36 ± 0.05	3.2 ± 0.5	7.0 ± 4.1	–	12.9 ± 0.3	11.7	82
B. pertusa	1.58 ± 0.02	2.1 ± 0.1	1.6 ± 0.7	10.2 ± 3.4	10.3 ± 1.2	329	526
D. annulatum	1.46 ± 0.2	1.8 ± 0.4	2.7 ± 1.0	3.2 ± 0.4	8.6 ± 0.9	98	265
B. intermedia	1.85 ± 0.08	4.6 ± 0.35	1.7 ± 0.8	28.6 ± 7.8	13.6 ± 2.0	474	805
C. fulvus	1.76 ± 0.08	3.7 ± 0.4	3.5 ± 1.7	–	22 ± 4.6	51	178
A. gayanus	3.21 ± 0.3	8.6 ± 0.8	29.6 ± 9.8	2	4.6 ± 0.2	22.7	672

Table 3. Dispersal unit characteristics and dormancy period in perennial grasses.

Species	Pedicelled spikelet L x W* (mm)	Pedicel length (mm)	Fertile spikelet L x W (mm)	Awn length (mm)	Caryopses L x W (mm)	Caryopses colour	Dormancy period (months)
Vetiveria	3.8 x 0.9	4.6	5.1 x 1.3	–	3.2 x 1.2	yellowish	3
Sehima	9.3 x 2.6	2.0	8.7 x 3.1	46	3.4 x 1.8	creamy	6
Heteropogon	4.2 x 1.3	2.1	4.6 x 0.4	85	2.7 x 0.4	creamy	6
B. pertusa	3.4 x 0.8	1.2	3.3 x 1.5	16	2.8 x 0.7	wheatish	3
Dichanthium	2.8 x 2.0	0.8	3.4 x 1.8	18	2.7 x 1.2	wheatish	3
B. intermedia	3.4 x 1.1	1.5	3.6 x 1.2	12	2.6 x 0.8	purple	6
C. fulvus	5.1 x 1.2	2.6	5.4 x 1.8	38	4.2 x 1.2	yellowish	3
A. gayanus	5.5 x 1.4	2.0	5.6 x 1.2	22	2.2 x 0.6	black	3

* L x W (length x breadth)

the spikelets. Standard conditions were used for all germination tests as per ISTA procedures (Ellis *et al.* 1985). The experiment was carried out in a seed germinator at 20/30°C (16h/8h) with 8 h photoperiod (3 x 40 w fluorescent tubes), during upper temperature per day. Spikelets/seeds (caryopses) were spread evenly on a 9 cm diameter, thick filter paper, placed in Petri-dishes. Filter paper were soaked in required quantity of distilled water (excess water was drained). No sterilisation treatments were applied to seeds/spikelets before germination tests. For each species, four replications each having 100 spikelets/seeds were used. In each case twenty one days were taken as a standard period for germination.

Results and discussion

Flowering phenology

Growth of pastures started immediately after the commencement of monsoon during June end and by the end of July *A. gayanus* and *V. zizanioides* attained a height of >90 cm, while in other species it varied between 60 and 80 cm. Flowering in *V. zizanioides* started after about 45 days of vegetative growth during mid-August and peak head density was observed during first week of September (Table 1). *S. nervosum* produced seeds during mid-September, while *H. contortus*, *B. pertusa* and *D. annulatum* started flowering in September and seed production began in October (Table 1). In *A. gayanus* flowering started after > 4 months of vegetative growth and seeds were produced during the second half of December. After harvesting the pastures during November/December (following seed collection), some inflorescences were seen in *H. contortus* (January - February) and *D. annulatum*, *B. pertusa* and *C. fulvus* (February - March). Other species flowered only once in a year. During winter - spring head density was low and heads were smaller in size, seed setting was poor, seeds were light and germination was low.

Inflorescence initiation in grasses primarily depend on photoperiod and exposure to low temperature, although majority of tropical grasses are considered to be indifferent to day length (Crowder & Chheda 1982; Humphreys & Riveros 1986). These tropical grasses seem to have a seasonal cycle which allows maximum vegetative growth during rainy season (July - September) followed by a period of seed production from September to December. Grasses flowering during August - September seems to be day neutral, while those which flowered during October - November, when day length was less than 12 h, appears to be short day species (Table 1). *A. gayanus* flowered once in a year (during April) in response to short days at a higher latitude site in Brasilia (lat. 15°, alt. 1000 m), while it flowered several times at the equatorial site, lat. 3.1, alt. 990 m (Ferguson *et al.* 1983). Tothill (1966) reported flowering in *H. contortus* in late summer and short days in north- eastern Australia. Temperature condition also affects floral induction, seed setting and its maturity (Humphreys & Riveros 1986).

Seed yielding components

Seed yielding component included are fertile tillers with apical and axillary inflorescences. Maximum tiller height and thickness was recorded in *A. gayanus*, followed by *V. zizanioides*. Tiller height was minimum in *H. contortus*, while tiller diameter was minimum in *S. nervosum* (Table 2). Height of *A. gayanus* sward was much higher than two m height recorded in S. Africa (Skerman & Riveros 1990). Dispersal units per head was maximum in *V. zizanioides* and minimum in *H. contortus*, but the number of heads per tiller was maximum in *Andropogon* (Table 2).

The dispersal unit

The dispersal unit is a diad in all species except in *C. fulvus*, where it is a triad (sessile spikelet is surrounded by sterile (pedicelled) spikelet on either side). A long drawn awn from the tip of sessile spikelet is prominent in all species except in *V. zizanioides* (Fig. 2). The awn is loosely held and some time get detached from the spikelets while stripping the spikelets for seed collection. Pedicelled spikelet of the diad is also frequently separated during seed collection except in *C. fulvus*. The pedicelled spikelets, commonly referred as sterile (without ovary) are considered to increase stamen - ovary ratio (Clayton 1990). The sterile spikelet constitute c. 30% of the total diaspore weight in *S. nervosum*, *A. gayanus* and *C. fulvus* (Fig. 3). In *A. gayanus* and *S. nervosum* weight of husk exceeds the weight of caryopses (Fig. 3). Awns, the most conspicuous appendages of the spikelets, are longest in *H. contortus* (70-80 mm). They accounted > 60% of total diaspore weight. The awns are straight in *C. fulvus* and *A. gayanus*, but spirally twisted in other species. In *Heteropogon* and *Sehima* green colour of awn is conspicuous during anthesis. The primary function of awn seems to facilitate germination by finding a suitable microsite, orienting the

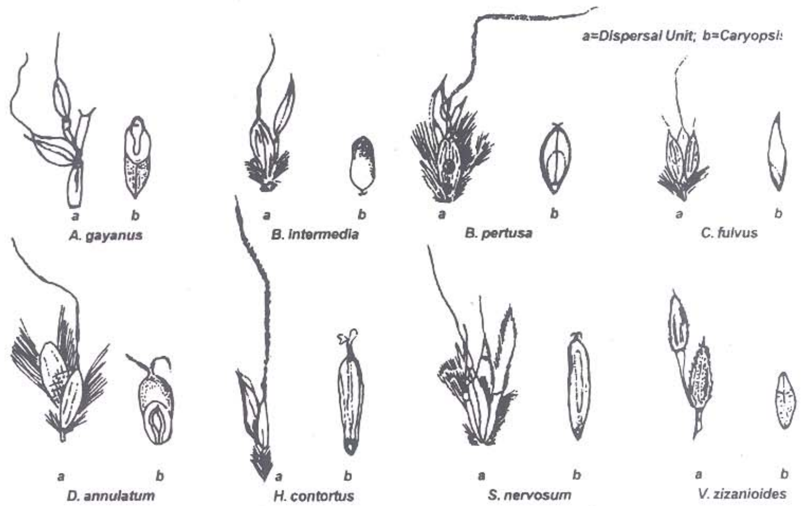

Fig. 2. Dispersal unit and caryopsis of eight tropical grasses.

seed for optimal moisture uptake and anchoring it against the thrust of emerging radicle. This is achieved by hygroscopic flexion or torsion which, combined with the on way devise of callus beard, drives the diaspore along the ground. This motion can be quite complicated when moving and static parts interact, and it has been shown to be associated with particular microsite preference (Peart 1984; Peart & Clifford 1987). Spikelet morphology plays a significant role in reproductive biology as most of the as-

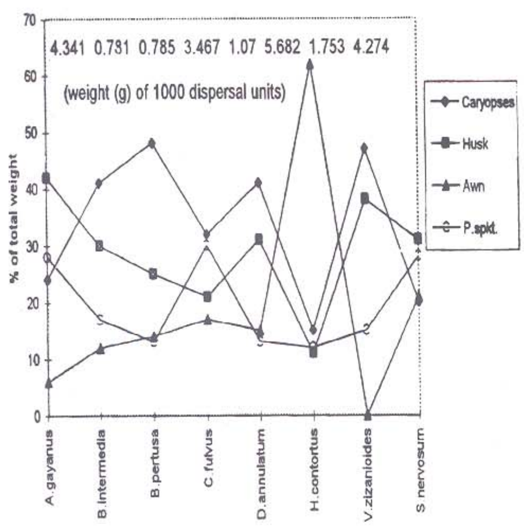

Fig. 3. % dry matter allocation in parts of dispersal unit.

similate transported to the seed is produced in the inflorescences e.g. awn in *Triticum* perform photosynthesis besides other function also (Grandbacher 1963). Maximum weight of 1000 dispersal units was recorded in *H. contortus* (5.682 g) and minimum (0.781 g) in *B. intermedia* (Fig. 3).

The caryopsis vary in size, shape and colour (Table 3, Fig. 2). In *Heteropogon, Sehima* and *Andropogon* caryopsis contributed 15, 20 and 24%, respectively towards total diaspore weight, while it was maximum c. 40-48% in case of *Dichanthium* and *Bothriochloa* spp. Weight of 1000 caryopses was maximum in *Chrysopogon* (1.098 g) and minimum (0.323 g) in *B. intermedia*.

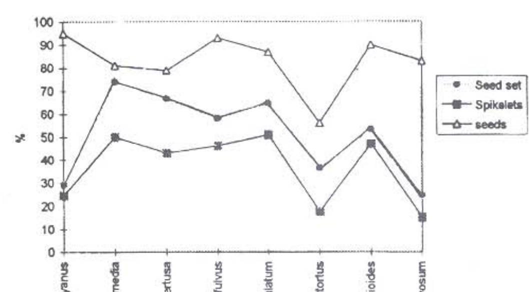

Fig. 4. Seed set and germination in spikelets and seeds (average of two years).

Seed setting and germination

Seed setting in spikelets determines the purity of 'seeds' and depend upon prevailing environmental condition during anthesis and grain formation (Humphreys & Riveros 1986). Grasses producing seeds during October-November showed higher seed setting and germination in spikelets as compared to other species (Fig. 4). Seed setting was poor in *Sehima* and *Andropogon*, therefore, germination was low in spikelets. Bowden (1964) have reported 60% seed setting in *Andropogon* in West Africa. Freshly collected spikelets required a period of 3-6 months for ripening before germination. Germination in spikelets ranged between 50 and 60% in *Bothriochloa, Chrysopogon* and *Dichanthium* (Fig. 4). Germination in seeds (caryopses) was 80-96%, except in *Heteropogon* where dehusking was difficult and some time caused damage. Vetiver was found to produce viable seeds contrary to the reports of its non-seeding type (NRC 1993). Per cent germination in spikelets of *Heteropogon* was also less in comparison to other reports (Tothill 1977). In general, seed setting and germination in spikelets was higher in grasses producing seeds during October-November, possibly due to favorable climatic condition in the form of sun shine and diurnal temperature regime during anthesis and seed formation. Seed (dispersal units) of all species qualify the standard regulation for seed quality of Queensland, which stipulate a minimum 10% germination and 30% seed purity (Boonman 1993).

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