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Flowering Mechanism in Kodo Millet (*Paspalum scrobiculatum*)

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Authors' contributions

This work was carried out in collaboration between both authors. Both authors read and approved the final manuscript.

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Review Article

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ABSTRACT

Since kodo millet is a self-pollinated plant, it is essential to understand the factors that influence the length of the flowering period, pollination behaviour, and seed set in order to improve breeding programme effectiveness and yield stability while also boosting productivity. Kodo millet flowers remain closed because they are cleistogamous in nature. They have tiny florets. Emasculation and artificial hybridization are challenging because pollen is less readily available. There are also only a few sources of information. To get around this, the current inquiry was started. It aims to gather fundamental data from a variety of sources of literature, and then, with the use of fieldwork this text was prepared.

Keywords: Anthesis; flowering mechanism; kodo millet; reproductive biology.

1. INTRODUCTION

Food production has to be increased from the present 240 million tones to 500 million tones by 2050 for the expected population of 1.65 billions in India. Since malnutrition is already prevalent in the country and food habits are changing towards quality food, fodder and feed production

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would have to increase more than double during the period to adequately feed the population. Tamil Nadu has a geographical area of 140 lakh hectares of which 52 to 54 lakh is cultivated. Of the gross cropped area about 50 per cent of the crop area is under rainfed conditions. Small millets nevertheless contribute to the regional food security of the dry and marginal lands, where main cereal crops fail to yield, thus an increased effort to enhance the acreage of these crops is crucial. Because millets are more nutritious than the other cereals, there is currently a push to grow them.

Among the small millets, important millet is kodo millet, which is a tetraploid (2n = 4x = 40; genome size 1.91–1.98 pg), belonging to the Plicatula group, family Poaceae, subfamily Panicoideae, and tribe Paniceae [1,2]. Indian-native kodo millet is a tropically produced crop that is grown for both grain and fodder [3]. It is a perennial, resilient, and drought-resistant crop [4]. Tamil Nadu and Uttar Pradesh have the highest productivity, while Andhra Pradesh, Karnataka, and Madhya Pradesh have the lowest [5]. Its production is primarily restricted to tribal communities, where it is grown in terrible conditions. Moreover, it serves as forage and livestock fodder.

Due to the prevalence of major cereals like rice and wheat, the area cultivated with kodo millet is seeing a downward trend in the post-green revolution era. When compared to other millets, Kodo millet has reportedly been shown to have a greater capacity to quench free radicals [6]. Also, it offers affordable protein, minerals, and vitamins in the form of wholesome meals [5]. Demand for these nutritional cereals, which are naturally anti-diabetic and anti-oxidant, is increased by consumers' growing health consciousness [7]. So, to increase the production of this crop on a viable scale, technological intervention is required.

Kodo millet is a self-pollinated crop, understanding of the parameters that affect the duration of the flowering period, pollination behaviour and seed set is prerequisite for increasing the productivity and yield stability as well as improving the efficiency of the breeding program for successful hybridization. Flowers of kodo millet are cleistogamous in nature and thus remained closed. Protogynous flowers occurs rarely in few genotypes. Only 5% flowers open and remaining being cleistogamous. The florets are very small. The pollen availability is also less which makes emasculation and artificial hybridization difficult. Hence, kodo millet has a very low level of variation and improvement due to the challenges in hybridization.

Although there is a lot of heterogeneity in the current germplasm collections, it has not been completely used. The crop has a number of advantageous traits, including increased herbage, branched inflorescences, more seeds per spike, excellent fertility, and an exceptional capacity for storage [8]. Even though the flowering mechanism of kodo millet is not clearly understand. Due to these, hybridization in kodo millet is quite difficult for plant breeders. Even though, some better cultivars have been developed and their production potential is limited. The variety CO 3 released during 1980 and then variety TNAU 86 was released during 2012, CKMV 1 and ATL 1 was released during 2020 and 2021 respectively by Centre of excellence in Millets, Tamil Nadu Agricultural University, Athiyandal. To overcome these barriers we need to clear understanding for flowering mechanism of kodo millet is essential. Keep this point in view, in this text is prepared with the field study of experience.

2. TAXONOMICAL CLASSIFICATION

In spite of its long history of cultivation, the variability seen in cultivated land races is very much limited. About 350 species in the genus *Paspalum* are grown for grain or as fodder, including *Paspalum scrobiculatum* L., *Paspalum notatum* Fluegge, *Paspalum conjugatum* Bergius, *Paspalum compactum* Roth, and *Paspalum dilatatum* Poir. *Paspalum sanguinale* Lamk is the ancestor of all wild *Paspalum* species. *Paspalum* comes in two types, *Paspalum scrobiculatum* var. *scrobiculatum,* which is cultivated in India as a significant annual crop. In mixed cropping, it is produced either as the sole crop or as the primary cereal. The wild variety of *Paspalum* native to Africa is *Paspalum scrobiculatum* var. *commersonii* and perennial type.

Based on the placement of the spikelets on the rachis, the three races of *Paspalum scrobiculatum*—regularis, irregularis, and variabilis—have been identified (Prasad Rao et al., 1993). Racemes of the Kodo millet are distinctive, with the spikelets in the race regularis organized in two rows on one side of flattened rachis. Race irregularis refers to the plant with spikelets grouped in two to four erroneous rows along the rachis. Some plants have two normal rows of spikelet arrangement on the rachis, while the lower portion of each raceme has irregularly organized spikelets. Variabilis race is the name given to these plants.

3. BOTANICAL DESCRIPTION

Kodo millet is a robust annual herb with tufts that can reach a diameter of 60 cm. Plants are 60-90 cm tall, thin to stout, and frequently root from the bottom nodes. Adventitious roots grow from lower nodes that have a lot of thin, shallow roots. Branched roots spread widely and laterally and continue to operate throughout the duration of the plant's life. The stem is tufted on a very short rhizome, erect, occasionally spreading or prostrate in habit, branching, and slightly succulent. Three types of growth habit erect, decumbent and prostrate has been observed in kodo millet genotypes (Fig. 1). Glabrous stem with totally sheathed internodes and swelling nodes. At a later stage, nodal bands turn purple. The first node is hairy, whereas the others have glabrous internodes and are glabrous. In all tillers, the internode length gradually grows from the bottom to the top. Depending on the genotype, there are five to 18 tillers. The basal leaf sheaths are either glabrous or pilose, and the leaf blades are simple, alternating, bifurious, upright or suberect, finely acuminate, glabrous or occasionally soft hairy, and up to 40 cm long. The 15–40 cm long, 5–12 mm wide, and light green leaf blades measure. Leaves and leaf sheaths are glabrous.

Spikes are 2-6 in number and 3-15 cm long. Spikelets are normally sessile or with short pedicillate arranged on a flattened rachis. The arrangement of spikelets is in two or more regular or irregular rows. The most common kodomillet is characterized by racemes with the spikelets arranged in two rows on one side of a flattened rachisis called as regularis type (Fig. 2a and 2b). Plats with irregularly arranged spikelets called as irregularis (Fig. 2c). Two kinds of aberrations occurs. In one kind, the spikelets are arranged along the rachis in 2-4 irregular rows (Fig. 2d). In the other aberrant kind, the lower part of each raceme is characterized by irregularly arranged spikelets, while spikelet arrangement becomes more regularly two rowed in the upper part of the raceme (Fig. 2e).The spikelets are flat, broadly elliptic, awnless with two florets of which the lower is reduced and rudimentary. Flowers are highly cleistogamous and self pollination is the rule. The grain is enclosed in hard persistent husk, which is removed after dehusking [9]. Raceme morphology allows for the recognition of three complexes.

4. FLOWERING MECHANISM OF KODO MILLET

Typically, the panicle develops from the node. A small protrusion of leaf sheaths is the first indication of the developing panicle. Through the sheath slit, the panicle is visible as the swelling gradually expands. It takes about a week for it to emerge. When fully emerged, it is surrounded by three leaf sheaths that overlap and roll inside one another at the top. In most situations, even when the panicle is in full bloom, the flag and the leaf behind it remain rolled at the top. Complete emergence of panicle has been shown in Fig. 2. The ends of the inflorescence are still stuck up in the previously stated inrolled area. The floral branches' upper ends are now fixed, and as they grow longer, their centres bend outward. The panicle's quick growth and ensuing arching cause the surrounding leaf sheaths to be driven apart until the tips are likewise forced out. This is the typical rule, but in the Sierra Leonean variation, the peduncles extend, clear the leaf sheaths, and hold the panicles high and away from them.

The other two bear panicles, with the exception of the lower three nodes. Three distinct peduncles emerge from each of the two higher terminals separately. The two lateral ones flourish while the central one fails. The one that fails has a sessile panicle. One or two branches of this panicle may bear primitive spikelets. One of the two freely expanding peduncles develops swiftly and emerges before the other. The earlier is consistently larger, contains more spikelets, and is less sterile. The spikelets at the ends of the branches of the later peduncle are typically sterile. Each of these peduncles produces three branches, one of which fails to develop; the other two exhibit similarly uneven growth and development. These branches continue in this trimestral pattern until little spikelet-bearing branches of varying sizes appear and blossom. Some of the abortives become long-stemmed single flowers during this final trimester. The stronger branches branch out and bear a greater number of blooms, whereas the weaker ones are generally unbranched. Up to 100 spikelets can be found at one time on a branch.

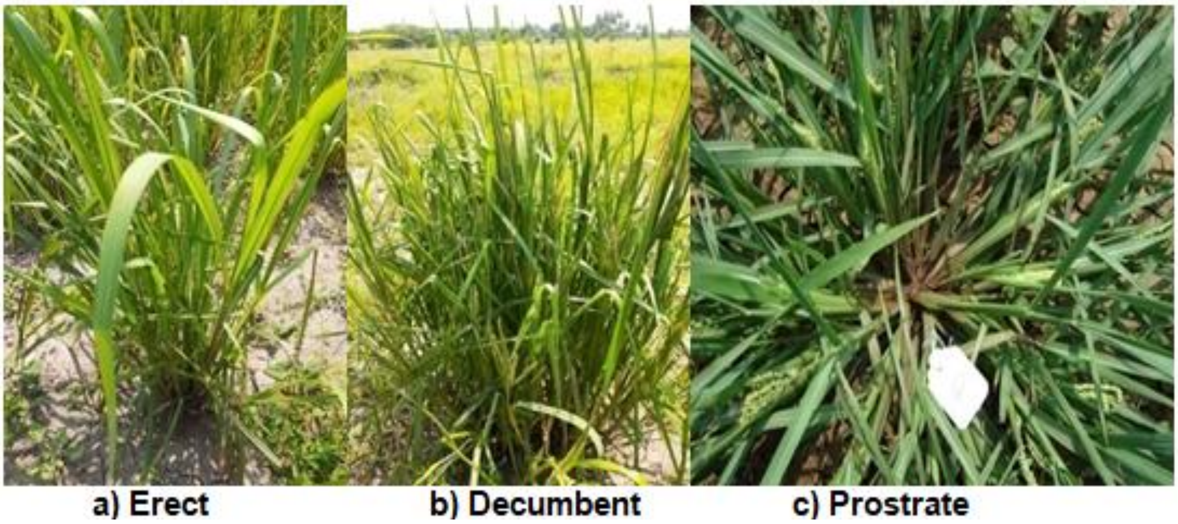

Fig. 1. Different growth habits of kodo millet

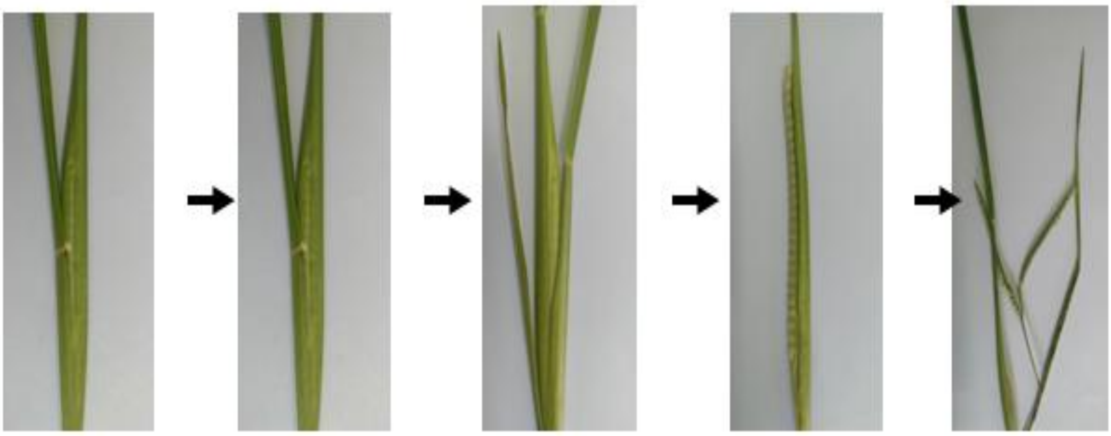

Fig. 2. Complete panicle emergence

Fig. 3. Panicle arrangement

A sequence of depressions that correspond to the placement of the spikelets are present on the broad, flat rachis of each branch. A central ridge extends the entire length of the side where the spikelets are located. The spikelets are placed alternately in two series on short pedicels on either side of the ridge (Fig. 3). In some types, a branching of the pedicel results in a non-seriateness, with the spikelets being organised erratically instead of the typical two-seriate condition. The branch is two-seriate at the bottom, non-seriate in the middle, and continues to be two-seriate at the tip.

In addition to the simple branching of the pedicel and the development of two blooms, the nonseriate condition can occasionally be detected running the full length of the branch.

(1) The pedicel forks into three parts, each of which has a spikelet rather than forking into two.
(2) It is capable of producing more than four flowers at various levels.
(3) On the ridge of the branch, small branches develop at various levels and produce a significant number of flowers.

The most significant element in the crowding and small size of the grain in earheads that are not two-seriate, in addition to the crowding caused by the branching of the pedicel, is the double seededness of such non-seriate heads. The reduction in the size of the spikelets is caused by the disturbance of two-seriateness, which also results in a dense packing of spikelets on the flat rachis. As a result, the spikelets in these are between one-third and fifty percent smaller than those in two-seriate panicles. The non-seriate variants are noticeable for being early, lighter in colour, and having husks with lighter brown grains.

This spikelet's description has been expanded upon from Hooker's Flora of British India, which does not include a description of the variety with double-seeded spikelets. Orbicular, primarily distinctly plano-convex spikelets fall abaxially from short, rudimentary pedicels on spike-like racemes' dilated rachis.

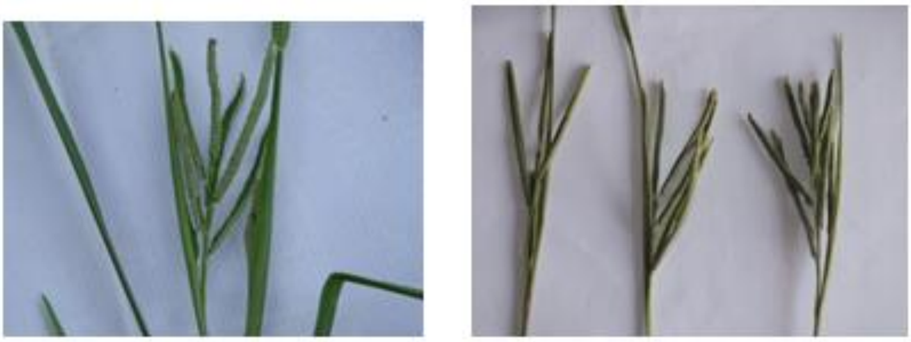

Fig. 4. Different View of Panicle Branches

Fig. 5. View of Regular, Irregular and Varigatum Types of Panicle

Glume 1 : 0 (suppressed.)

Glume II : Convex, membranous, light green, and almost equal to the spikelet. They are also deciduous, glabrous, and 5–6 nerved.

Glume III : Similar to Glume II. but less convex and more flat; light green; thin; glabrous deciduous; 2-5 nerved; along the inner margins are seen shallow transverse pits, hence the specific name "scrobiculatum".

Glume IV : Horny, light green in colour, eventually turning light or dark brown, glabrous, with five translucent nerves; solid; obtuse; emucronate; persistent.

Palea : Similar in content to Glume IV; tightly encompassed by the narrowly involute borders of Glume IV; 2 transparent nerves; the palea with flaps enlarged into a broad auricle below the middle: persistent.

Stamens : Three; filaments short, 1 m. m. long. anthers-3, 2-3 mm. long; 2-loculed; locules open by longitudinal lateral sutures .

Ovary : Ova1; translucent; stigmas··2. styles distinct and laterally exserted near the tip of the floret; styles feathery from one-third the length from the apex

Lodicules : Two; fleshy; serrated tips; broadly cuneate.

Grain : glume and palea tightly enclosing the rotund-elliptic shape, which is highly convex in the front. whitish, flat on the back, and with a scutellum that is half as long as the grain.

Spikelet : Seeded twice. Between Glume II and the palea of Glume IV, an extra flower is interpolated in the double-seeded spikelet. A second glume and palea are used to enclose it. Each spikelet produced by this additional bloom contains two seeds. Together with this twofold fertility, abortion-related situations of this double seededness freely emerge and take the following forms. Between Glume II and the palea of Glume IV, an additional bloom grows. It is a flawless blossom with just one additional palea. No seed is established.

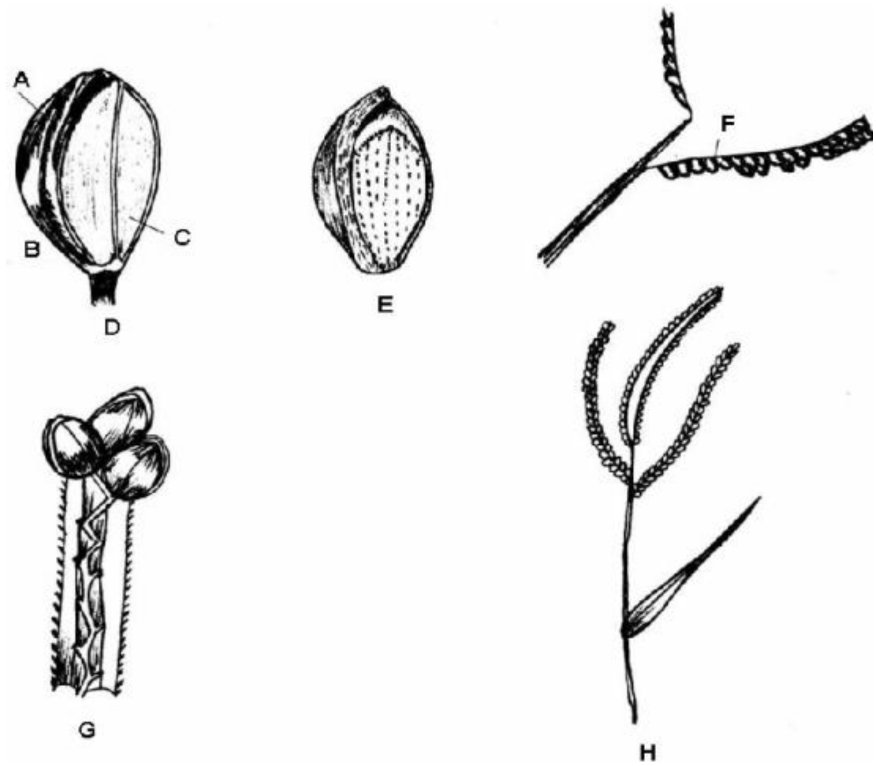

Fig. 6. Floral parts of Kodo millet

(A) Upper floret; (B) Second glume; (C) Lemma of lower floret; (D) Spikelet; (E) Floret; (F) Rachis; (G) Arrangement of rachis in spikelet; (H) Inflorescence.

5. OPENING OF THE FLOWER

Typically, the first flower opens on the second day following the panicle's emergence. Every day, between 2:30 and 3:00 a.m., this blossoming starts and lasts until sunrise. Kodo millet is cleistogamous, although some genotypes, including IPs 147, 197, 427, and others, have been shown to exhibit protogyny. Approximately 5% of flowers open; the others are cleistogamous. According to Youngman and Roy (1923), these flowers bloom in Nagpur between 7:30 and 8 a.m. Flowers don't start to open at one specific place. Typically, they begin in the centre of the flowering branch and move outward gradually to either end. There are rare cases where flowers start to bloom at the ends.

6. ANTHESIS OF A FLOWER (ANTHERS EXTRUDED)

Above are detailed observations on anthesis in a regular, average flower that indicate the regularity of order.

2.30 a.m - Glumes begin to open.
2.40 a.m - Anthers visible through opening.
3.15 a.m - Anthers emerge.
3.30 a.m - Anthers completely out.
3.35 a.m - Anthers dehisce.
3.45 a.m - Glumes close completely.

Stigmas might or might not emerge from the glumes. The anthers end is near the orifice and become un-dehisced when the glumes start to gape. Most of them do not emerge. The length of their filaments is 1 mm. Anthers with 6 mm-long filaments occasionally develop. These filaments are stiff for a long period, frequently until 8 or 9 in the morning. The anthers can open all at once, one at a time, two at a time, and then three at once. The lack of flowering indications in this inconspicuous millet is explained by this stray emergence. When the anthers are still inside the flower, their dehiscence happens after the glumes have opened for a considerable amount of time. Dehiscence may begin as a slit at one end and gradually expand to the other, or it may start in the middle and move outward. In the evening, the stigmatic feathers are dry. The anthers do not deteriorate and are still fresh the following morning. The fleshy lodicules do not instantly shrink following flower anthesis; instead, they stay fleshy for 6 to 8 hours after the opening of the glumes before drying up, possibly as a precaution from closing glumes obstructing the anthers [10].

7. PROGRESS OF FLOWERING

The following table connotes the daily anthesis energy of the 15 per cent of flowers opening during the flowering period, emerging and non-emerging anthers included.

Days of Flowering	2-3 a.m	3-4 a.m	4-5 a.m	5-6 a.m	Total
First day	14	1	1	-	16
Second day	2	10	-	1	13
Third day	7	11	-	-	18
Total	23	22	1	1	47

**15 per cent of the flowers in the head opened. The remaining 85 per cent were cleistogamous*

All of the flowers in the head will not open, as can be seen. In the different types, the proportion of open flowers ranges from 0% to 50%, with 10% to 15% being the most common. Given its high degree of cleistogamy, the absence of any natural crossover in this millet can be explained. Any artificial manipulation of the spikelet permanently destroys it, and numerous attempts at artificial pollination and emasculation have been ineffective.

At Rewa, Madhya Pradesh, Verma [11] discovered that the ideal timing for anthesis is between 05:45 and 07:30. A single panicle floret opens for 20–30 minutes during this time. When flowers are in anthesis, the stigma emerges first, and anthers follow immediately. Yadava [12] used a protogynous-induced mutant to study the flowering behaviour of kodo millet (KM 32). In this mutant, the third day following the end of panicle emergence marks the beginning of flower opening. Beginning in the middle of the panicle, flowering spreads to both sides. A panicle's flowering takes over a week to finish. The best flowering period was between 0600 and 1130 hours. Anthers' dehiscence occurs after they turn from whitish to light yellow in colour. In the Indian wild types, the spikelets' stigmas protrude (Doggett, 1989). Under Athiyandal climatic condition the time of anthesis in kodo millet is 05:30 and 07:30 hours. Open of single spikelet in a panicle takes 20 -30 minutes.

8. GRAIN

The grain matures 30–35 days after flowering: The fourth hardened glume and its palea completely encircle it. Several tones of brown make up the husk. Compared to the non-seriate types, the grain in the two seriate kinds is larger and almost twice as large. The grain is tiny even if the head is two-seriate in the above-mentioned cultivar brought from Siena Leone. With both heads having roughly the same level of sterility, the level of head emergence has no bearing on how the seed will set. Seasonal factors determine when millet seeds are set. The drought of 1928 severely impacted some types' ability to set seeds, making it impossible to harvest even a small number of grains per plant. Good yields might be anticipated in favourable conditions. The stiff and thick seed coat of varagu crop generally results in poor milling output. The milling out turn will be substantially greater for uniformly sized grains with thin seed coat layers and easy threshing capabilities.

9. FLORAL MORPHOLOGY

The inflorescence of kodo millet is made up of 2–6 racemes that spread out widely along a short or sub-digitate axis. Racemes measure 3 to 15 cm in length [13]. Very often sessile or on a short pedicel, the spikelets are. In a rachis that has been flattened, they are often two rows of one [14]. Many spikelets are paired in the raceme's midsection. Ribbon-like, 1.5–3 mm broad, and with scabrous borders, the rachis looks like a ribbon. The two series of spikelets, long and short pedicelled, are alternately placed [15]. The glume II is the same length as the spikelet while the glume I is missing. Because lemma II encloses both florets, lemma I is essentially identical to glume II. The higher floret in the spikelet is a hermaphrodite flower, while the bottom one is sterile and reduced to a valve [16]. Hard, horny, persistent husks enclose the grain [17].

10. ANTHESIS AND POLLINATION

Kodo millet has a cleistogamous bloom [12], and as the amount of open flowers is typically between 15 and 20%, self-pollination is the norm. Raceme's middle-located spikelets open first, then slowly spread to its ends [16]. From 2:30 a.m. until dawn, Spikelet is open [18]. Because of how tightly the lemma is wound, any attempt to artificially manipulate the florets open will result in flower damage. Several Kodo millet cultures, such as IPS 147, IPS 197, and IPS 427, have been found to practise protogyny [11]. There are recognised apomictic species in the genus Paspalum [19]. Yet, there are no reports of this characteristic in Kodo millet.

Fig. 7. Brown colour husk of grain

Fig. 8. Variation in Panicle Morphology

11. FALSE POLYEMBRYONY

Two occurrences of two seedlings growing from a single seed were seen in this millet in the year 1931, during a number of seed germinations for albinism. The seedling had two plumules, each with its own coleoptile, and one root. The two were distinct at the seed's surface. The plumules' separate vascular bundles were visible in paraffin seed slices. The cortical parts of the two shoots were observed to merge lower down, whereas the bundles ran independently. The vascular bundles were closer and moved in closer proximity to one another in a few lower areas before becoming encased in a single endodermis. The root strand was visible running into this single bundle in sections even further below. What appears to be independent at the top is actually the consequence of the branching of a single seedling, as can be observed from this inspection of the course of the vascular bundles and also of the cortical region. The mesocotyl has split into two at a very early stage of development, making the double seedling a false polyembryony. Some researchers have noted instances of pseudo-poly embryony. Only those connected to the Gramineae are apparent. In the case of maize, Kiesselbach [20] observed seedlings with either: (1) two plumules, each with a separate coleoptile and two primary roots encased in a single coleorhiza, or (2) one plumule with two primary roots in a single coleorhiza. There are two plumules in the example being discussed here, each having their own coleoptile but only one radicle.

12. WIDE HYBRIDIZATION

***Paspalum sanguinale,* Lamk:** Many *Paspalum* species are cultivated as pasture grass in America, Australia, and South Africa, particularly *Paspalum dilatatum.* In the Vizagapatinam District, a wild *Paspalum* ally known as Chicco (*Paspalum sanguinale*, Lamk) is grown. This was raised for a period of years at the Millets Breeding Station, TNAU, Coimbatore. Two days longer than Varagu, the very small seed takes 7 days to sprout. The seedlings are green and lack any purple pigment throughout the plant, in contrast to *Paspalum scrobiculatum*. The plants are spreading and nearly prostrate before blossoming. At flowering, the tillers that carry panicles stand upright. The internodes, unlike varagu, are hollow and extensively exposed. They are a golden yellow colour when fully mature. The nodes are not enlarged and are glabrous. The flag leaf is the plant's largest leaf. The lower surface of leaves is smooth, whereas the upper surface is rough. The leaves are not bowed; they are arched. The plants feature five to six heads with long, straight peduncles that are well-emerged. Sometimes their fullness causes goosenecking. The panicle resembles a fully developed *Chloris barbata* in general. It is made up of several fingers (or branches) arranged in haphazard whorls along a small axis. There may be 40 fingers on an average earhead. The majority of them originate from the two bottom whorls, with the remainder spread to those above, primarily in groups of two and three. There may be 100 blossoms on each finger. The length of each spikelet is four to five times its width, making them incredibly tiny. The glumes have noticeable ribs and turn straw-colored when dried. The spikelet has a similar structure to all other *Paspalums*. This wild ally's blooms open between the hours of one and three in the morning, and anthesis lasts until seven. Within the first hour of opening, there is the most anthesis energy. A panicle finishes flowering in four to five days. More herbage, unattached earheads, greater drought resilience, more seeds per head, and lack of sterility are some of the ways that this wild *Paspalum* outperforms *Paspalum scrobiculatum*. If the challenges associated with handling this little, fragile cleistogamous blossom could be addressed, a cross with this wild ally is suggested as a potential source of improving the kodo millet [21].

Germplasm maintenance: The advanced cultures of varagu crops received for evaluation from AICSMIP, Bangalore and Departmental of Millets, TNAU, Coimbatore were included in the germplasm pool. The seeds collected during field visit to different places were also added to germplasm collections. The following materials were conserved as germplasm accessions. These materials were sown for purification and multiplication.

A total of 4303 germplasm materials in seven small millet crops including Browntop millet have been documented at Centre of Excellence in Millets, Athiyandal. A total of 393germplasm accessions in all the seven small millets were evaluated during 2021 to validate their significant attributes to be utilized as working germplasm. A few of the trait specific accessions were utilized in the crossing programme. Along with the traits for yield increase, pest and disease resistant, bio-fortification and value addition lines were also sourced for crossing.

S. No.	Crop	No. of germplasm documented
1	Finger millet	2263
2	Little millet	196
3	Barnyard millet	269
4	Kodo millet	197
5	Foxtail millet	864
6	Proso millet	424
7	Brown-top millet	90
Total		**4303**

S. No.	Crop/Traits	Mean	Range	Selected Accessions
1	**Kodo millet**			
	1000 Grain Weight (>4.2g)	4.3	2.9-5.8	TNPsc 176, RPS 564, GAK-13
	Duration (95-100 days)	102.0	94.9-138	TNPsc317, RPS 694/3, BK 1-48-2
	No. of Prod. Tillers/Plant (>15)	7.0	1-18	BK 43, RPS 92, KMNDL- 4-1
	Panicle Length (>18.5 cm)	14.6	10.3-16.9	TNPsc262, RPS 694/4, TNPsc 313

COMPETING INTERESTS

Authors have declared that no competing interests exist.

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