KNOB PATTERN AND ITS RELATIONSHIP WITH QUANTITATIVE CHARACTERS IN MAIZE: A REVIEW

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ABSTRACT

The present review on knob pattern and its quantitative character relationship in maize (Zea mays L) has been written covering the research work done on its various aspects. The topics included, pachytene analysis, global distribution of knob (knobs in Indian maize; knobs in exotic maize and knobs in relation to altitude); combining ability in relation to knob; gene action and degree of dominance for knob, heterosis in relation to knob number and grain yield, knob inheritance, cytoplasmic effects, correlation studies among knob and agronomical traits in maize in rainfed. Knob and its relation with other aspects have been critically reviewed.

The award of the Nobel Prize to Dr. McClintock, the first to receive the honor for work with a higher plant-maize (Zea mays L) was the occasions of pride and is a source of great inspiration to all the biologists of the world. The topology and topography of the gene has been under the constant study. Heterosis is the foundation of hybrid breeding in maize, but little is known about its genetic basis. East (1908) and Shull (1909) suggested that heterosis for yield and other heterotic traits is a function of heterozygosity at a large number of loci, enhancing the number of heterozygous loci by crossing less related lines or populations, generally increases the level of heterosis observed in crosses at least over a wide range of geographic diversity. The importance of hybrid power in maize has been so drastic that it is often quoted as one of the significant achievements of plant breeding efforts in the 20th century. The breeding of superior hybrids, composite and synthetic largely depends upon the judicious selection of superior parents. The ultimate factor that determines the usefulness of the parents for the hybrids is their combining ability. General and specific combining ability analysis is useful to ascertain the genetic worth of parents in hybrid combinations (Sprague and Tatum, 1942).

The chromosomes of maize are well known for containing heterochromatin, revealed usually as "knobs" at the pachytene stage of meiosis (McClintock, 1929; Longley, 1939; Rhoades, 1950). The number and distribution of these heterochromatric knobs have contributed to the development of maize cytogenetics (Longley, 1941; Rhoades, 1974). Knob heterochromatin is composed of a 180bp repeating unit arranged in random array (Peacock et al., 1981) and Chugtai and Steffensen (1989) recognized GAAAT repeated sequences. These attributes transmit like a gene (McClintock et al., 1981). The high knob races are restricted to the lowlands while low knob races are restricted to high land races. Apparently the amount of knob heterochromatin is related to the growing season and thus to the adaptation of maize to its environments, the knobs determine the hybrid performance. The knob number and their position may be used as cytological markers (McClintock, 1978). Knobs are related to the combining ability of the inbreds and that knob heterozygosity is a factor in heterosis, knob polymorphism in open-pollinated varieties of maize is expected and is partially responsible for their relative success. It is more exact specifications, more productive and less expensive.

Pachytene analysis: McClintock (1978) reported that no other stage of cell division, meiotic or mitotic, provides the detailed picture as the pachytene stage for the analysis and the identification of chromosome of maize has been so widely accepted as to almost become a dogma. Woolwood and Randolph (1957) stated that clumped vs well spread pachytene character does not follows a simple Mendelian inheritance and it probably is polygenic in nature.

Global distribution of knob: Knobs are always found at fixed positions and their racial and

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geographical distributions are highly non-random. Different races of maize possess different sets of knobs and in many cases knob combinations are distinct in races from adjacent regions (McClintock et al., 1981).

(i) **Knobs in Indian maize**: Extensive variability in plant, tassel, ear characteristics and knob polymorphism are observed in genotypes of Northeastern and northwestern highlands of India. However, the collections from plains did not exhibit much variability. Jotshi (1982) reported 20 knob-forming positions and the mean knob number for the varieties of Kashmir, being grown in two districts of Anantnag and Baramulla, being 7.64. The most frequent knob present being 5L, followed by 6L, 1L, 4L and 8S respectively. The location 2S, 4S and 6S were most rare. Jotshi and Patel (1983) reported 36 knob-forming positions in 15 local maize varieties of Kashmir. The average knob number of different varieties growing in Anantnag, Phulwama and Baramulla was found to be 30, 29, and 31 respectively. The highest knob number (32) was reported in "Badeh V" variety, followed by Tripathi (28), Vozji (28), and Niver (18) varieties. One significant new terminal knob position on 2Lt. was identified. Dash et al. (1986) observed 12 knobs in Muralia, a Sikkim Primitive maize collected from Pithoragarh of U.P. hills bordering Nepal. It has prominently large knobs at 2L, 4L, 5L, 6S, 7L, 8L, 6Lb and 6Lc (where L stands for long arm) positions showed smaller knobs. Kumar and Sachan (1992) reported knob polymorphism of 50 maize collections from North eastern hill region. Several new knob positions, unknown in American maize races, were identified. These are 1Lb, 2Lb, 2Lt (Long arm and terminal) and 9Lb. Kumar and Sachan (1994) presented the chromosomal polymorphism in 45 native maize races of NEH and discussed about the presence of heterochromatic block, satellite and new knob forming position. Kumar and Sachan (1997) reported various knob frequencies in different areas of northeastern hills. Maximum number of knobs were present in maize collections from Tripura (20) followed by Nagaland and Sikkim (18), Meghalaya (16), Arunachal Pradesh (11) and Assam (9). Four new knobs position 1La, 2Lb, 2Lt and 9Lb were identified in Tripura, Meghalaya and Nagaland respectively. Kumari (1997) observed 9 knobs in pollen karyotype of the maize genotype MS1DR-120 on 3L, 6La, 6Lb, 7L, 8L, 9L, 3S, 6S and 7S (where S stands for short arm) at Dholi (Muzaffarpur).

(ii) **Knobs in exotic maize**: Knobs on maize chromosomes exhibit a North South pattern on distribution in the U.S.A. (Longley, 1938; Brown, 1949). Thus the northern flints have few, if any knobs. The number in the southern dents ranges from 8 to 12. The knob number in the mid west dents varies from 3 to 5 and their overall distribution is intermediate between that of the northern flints and southern dents. Mangelsdorf and Cameron (1942) reported 7.9 and Reeves (1944), 9.25 as the average knob number for maize in Guatemala. Mangelsdorf and Reeves (1944) suggested that maize have developed as a highly domesticated plant in the Andean region and was spread from there to all parts of south, central and North America. Its chromosomes were knobless, but during its migration northward it became hybridized with Tripsacum (a related genus with knob chromosomes) in central America, from those hybrids new types of knob by chromosomes were derived, Wellhauseen et al. (1952) reported that all ancient indigenous and pre-Columbian exotic races had relatively low knob number, usually six or less, where as all are pre historic. Mestizos and modern incipient races had a relatively high knob number, usually more than six. Ono and Suzuki (1956) reported similarity between karyotype of Nepalese maize and that of Japanese and American maize. They reported knob number in somatic chromosomes ranging from 9-16, with the mean of 9.1. They suggested that Nepalese maize is closer to the non-Andean type, Ibrahim (1960) observed upto 3 chromosomes knob in his collection from regions north to 40° north latitude. Based on Longley and Katto's studies (1965), two general groups or complexes of primitive races can be recognized. The first group includes races with a high knob number and predominantly large size knobs, like Nat-Tel, Chaplote, Pira, Maicena, Apollo, Guarnbero, Canilla, Araguito and Sabanera. The second group of races are characterized by presence of generally low number with a predominance of small size knobs, e.g. Palameno Tolueno, Conife Morocho, Conife Puntagiudo, PisínKalla, PisínKalla-Pororo, Canguil and Euano. The Mexican races have more complex patterns of knob distribution (Kato, 1976;
McClintock et al., 1981). Many tropical and subtropical open pollinated varieties have 12 to 16 different knob combinations, often heterozygous (McClintock et al., 1981). Anguir-Perecin and Decico (1988) showed that some inbred lines derived from Jack-duro, a commercial flint variety in Brazil, were segregating for some knob after 4 or 5 selfing cycles. Chugtai and Steffensen (1989) observed 1 to 6 knobs with most lines having 3 to 5 knobs in American commercial varieties. The mean number was 3.23, a large knob on the long arm of chromosome 7 was the most frequent (90%) followed by the one on the long and short arms of chromosomes 4 (82.5%) and 9 (45%), respectively. Tsisogenetika (1990) observed knob polymorphism for distribution, size and seen as one of the mechanism regulating mode of reproduction in allogamous crops. Wan et al (1992) reported 4 and 8 knobs in Mo17 and FR16 respectively and H99, Pa91 and B73 all had 12 knobs including nucleolus organizing regions.

(iii) Knobs in relation to altitude: Mangelsdorf and Cameron (1942) have noticed that within each locality in Guatemala there is a wide variation in altitudes and the form of maize occurring at lower altitudes are triasicoid in nature and have a greater number of knobs than the form occurring at higher altitudes. Corn, that is adapted to either high latitudes or altitudes tends to have a low number of knobs while that found in either low latitudes or altitudes has a high number of knobs (Longley, 1938; Brown, 1949). The varieties adapted to the lower elevations have a higher average knob number than the varieties adapted to the higher elevations (Wellhausen et al., 1951). The reduction in knob number at high altitudes has been shown to occur in Mexican maize by Wellhausen and Prywer (1954). At higher altitude there is cold and maize adapted to colder climate requires lesser number of the knob. Knob number is distributed according to the altitude in an area with low-knobbed or knobless strains restricted to the higher altitudes (McClintock, 1960). Pandey et al. (1988) observed significant differences in knob number among the strains collected from different altitudes of Sikkim ranging from 1200 to 2500m. Strains occurring at higher altitudes of Sikkim possess fewer knobs in comparison to the strains at low altitude. The Sikkim Primitive strains have been classified into two groups, one having knob number (S-12), distributed in Sikkim and Tripura and the other with lower knob number (1-4) represented by the strains from Meghalaya.

(iv) Combining ability in relation to knobs: Since there is optimum number of knobs for specific altitudes, the inbred with different number of knobs will exhibit different trends of combining abilities depending on the location of testing. Wellhausen and Prywer (1954) observed that the higher knobbed ones within each variety tended to be the best combiners in top crosses. The highest yielding inbred lines in top crosses on an average had 1.12 more number of knobs than the low yielding ones. At low altitudes, high-knobbed inbred performed better in crosses than low-knobbed lines. Reid's yellow dent and Lancaster sure corn, originated from similar cross between a late southern dent (high knobbed) and an early flint (low or no knob) (Wallace and Brown, 1956; Baker, 1984). The best combining ability was observed between the knobless lines and the knobbed lines (Mohamed and Shoeb, 1965) where all the knobs were in heterozygous condition. Since there are no knobless lines in commercial use in the U.S. corn belt, the inbred with only one or two knobs are expected to be the best combiners. The best hybrid combinations resulted from out crossing higher or medium knobbed lines to knobless (Kalsay and Sharma, 1970). Moll et al. (1972) stated that knob heterozygosity/homozygosity plays an important role in combining ability. The best combining ability were observed between the knobless and the knobbed lines (Rakha et al., 1979). The inbreds with low knob number are expected to combine well even with the inbreds, which are related genetically but have a different knob constitution, that is, a medium or higher knob number. That Mo17 combined well with Oh43 related inbred (Via50, Oh40B, Va26, and Oh545). Free et al., (1986) and Steffenson (1987) reported that the low knob number Lancaster inbred (CV103 and Mo17) have wide range of combining ability. The French inbred, F, is another near-knobless type which has a wide range of combining ability expected on the basis of knob constitution. It is one of the most extensively employed inbred for developing the cold tolerant hybrids in Europe. The knob DNA in gene expression could explain the geographical distribution of the knobs and might provide clues
to understanding the dilemma of combining ability. Sajjad et al., (1955) indicated that knob frequency is closely associated with combining ability of maize genotypes. Generally, the best hybrids result from crossing high (or medium) knob genotypes with knobless or low-knob genotypes.

(v) **Gene action and degree of dominance for knobs**: The genetic make up of an attribute comprises of additive, dominance and epistasis. The information of the relative degree of genetic variance components is fundamental in the selection of appropriate breeding methodologies. A number of studies as reported on grain yield and knob that have shown the prevalence of different type of gene action. Mandal (1998) observed that both gca and sca were important for inheritance of knob.

(vi) **Heterosis in relation to knob number and grain yield**: Genetic diversity arises due to separation or due to genetic barriers to crossability. In plant breeding, it plays an important role because hybrids between lines of diverse origin, generally, display a greater heterosis than those between closely related parents. Yamasaki et al., (1957) found that in crosses between inbreds derived from the North American dents and Japanese flint (usually knobless) the degree of heterosis was directly proportional to the number of heterozygous knobs. This was true even for the crosses between inbreds with related pedigrees. Knob heterozygosity might plays a role in heterosis as proposed by Bianchi et al., (1963). The best hybrid combinations result from crossing of high-or-low medium knobbed lines to knobless (Mohammed and Shoeib, 1965; Rakha et al., 1979) or low-knobbed lines (Kalsay and Sharma, 1970). Moll et al., (1972) stated that knob heterozygosity/homozygosity plays an important role in heterosis. In a series of reports on interspecific hybrids in maize (Eubanks, 1986, 1987, 1988), it has been observed (a) transportation of knobs from terminal to internal positions, (b) knob amplification and (c) interconversion of knob from heterochromatic condition and vice versa. Chughtai and Steffensen (1987) hypothesized that knob DNA in gene expression could explain the geographical distribution of the knobs and might provide clues to understanding the dilemma of hybrid vigor. Chughtai (1988) indicated that knob heterozygosity plays a significant role in heterosis, as well as intolerance to inbreeding in tropical and subtropical maize material. Beck et al., (1990) evaluated diallel cross and recorded that average heterosis was significant for grain yield. Yield heterosis over the better parent was low in most of the crosses. Vasal and Srinivasan (1991) suggested the breeding strategies in hybrid development should consider the use of both inter and intra population crosses to exploit the broad genetic variability found in CIMMYT germplasm. Bhatnagara et al., (1993) observed significant differences among entries for the characters under study. Heterosis as per cent over mid parent, ranged from 21.3 to 55.0 per cent and was significant in ten crosses for grain yield.

(vii) **Knob inheritance**: Knobs are structural components of chromosome organization and are inherited in the same way as the gene (Rhoades and McCilintock, 1935; Rhoades, 1955). Mangelsdorf (1947) suggested that knobs themselves may have no genetic effect but that associated with them are segments in maize. However, evidence of inheritance of such chromosome segments or blocks or genes, which behave like single genes has been reported by him. It has been shown by Brown (1956) that the number of knobs in inbred, which underwent selection, was higher than those, which did not undergo selection. Blumenschain (1964) studied on segregating progeny from a cross between the knobless Wilbur's flint and high knob Zapalote Chico. The F2 plants heterozygous for knobs have higher means than homozygous and knobless plants for almost all knobless plants for almost all plant characters. The key observation was that none of the knobless homozygous were superior to the knob heterozygous regardless of the new gene combinations generated by recombination. In a series of reports on interspecific hybrids in maize (Eubanks, 1986, 1987, 1988), it has been observed (a) transportation of knobs from terminal to internal positions, (b) knob amplification and (c) interconversion of knob from heterochromatic condition and vice versa. Angui-Perecin and Decca (1988) showed that some inbreds lines derived from Jackdwo, a commercial flint variety in Brazil, were segregating for some knobs after 4 or 5 selfing cycles.

(viii) **Correlation studies among knobs**
and agronomical traits in maize: Correlation coefficient is a measure, which is used to find out the degree (strength) and direction of relationship between two variables. Brown (1949) observed that the high knob number is correlated with high kernel row number, row irregularity, denting, absence of husk leaf, and many seminal roots. Brown (1949) observed a positive correlation between number of knobs and row number (significant at 0.05 level) in Southern dents maize. The correlation coefficient between knobs and dents were +0.20, significant at 0.05 level. Flag leaves area were inversely correlated with number. He also observed rather close association between knobs and seminal roots in open-pollinated Northern flints and Southern dents and some slight association between these characters in corn inbreds. Shape for maize containing 5 knobs were pyramidal and cylindrical or nearly so have fewer than five knobs. The ears of most Southern dents are distinctly pyramidal; whereas the low knob Northern flints were typified by cylindrical ears. Vachnani (1950) has made for the interrelationship between knob number and nearly all the agronomical and morphological characters of some inbred lines. No significant association was found, although some of the ear characters approached the five per cent level of significance. Ibrahim (1960) investigated that high knob number was highly associated with the large kernel size, the correlation coefficient between these two characters was $r = 0.696$, there was an indication of positive association between high knob number and each of denting and high kernel row number. The correlation coefficient between high knob number and high kernel row number was $r = 0.041$. Moll et al., (1972) observed the effects of four knobs, 2L, 6L3, 8L1 and 9S in the yield, ear and plant height, and number of ears per plant in crosses of 18 inbreds heterozygous for each of the four knobs resulted in higher yield, ear and plant height, and number of ears per plant as compared to the homozygous. The 9S knob homozygotes were drastically reduced in yield. Even in heterozygous condition yield was lower than the homozygous knobless state. In order to meet maturity requirement, it seems desirable to leave certain knobs in a homozygous condition, the 7L knob is most likely to be homozygous followed by 4L and 9S in corn belt hybrids (Kato, 1976 and McClintock et al., 1981).

Chughtai and Steffensen (1987) reported that each homozygous knob combination delays plant development (pollen shedding) by three to four days. A heterozygous knob has no delaying effect. The number of homozygous chromosome knob sites was correlated with leaf number at maturity. Southern and Mexican races, with 6-16 knobs, had the most leaves. It is suggested that knobs delay flowering by increasing the number of leaves initially. All commercially successful inbreds, with very few exceptions, have a large 7L knob and most, with the exception of early. Lancaster derivatives, have a large 4L knob. B14 and most of BSSS-related and Oh43 related inbreds have a 9S knob. A heterozygous knob has no delay effect. Thus, the delay in development and the later time of flowering is positively correlated with the number of homozygous knobs. Steffensen (1989) observed that the longest ears were found only on plants flowering in the early, indicating heterozygosity for all knob loci regions. Sajjad et al., (1955) observed that hybrids with 91 and 105 days to pollen shedding, have 7.70 and 13.84 knobs respectively and less knob number has higher number of ears per plant and vice-versa.

(ix) Maize in rainfed: Maize being traditionally a kharif crop has to face several environmental stress especially drought and waterlogging due to excessive monsoon showers. Borodin et al. (1988) observed that the most stable heat, drought and salt resistance was shown by hybrids in which maternal parent was highly resistant. Kato (1976) discussed the possibilities of use of morphological and cytological classification in investigations of adaptability. Variation in the copy number of repeat sequences at a particular knob position between different N.E.H. regions may be attributed to the adaptation to a particular environment (Kumar, 1990). These results can lead plant breeders to utilize traits as indirect selection criteria for yield in specific environments.

CONCLUSION
Knob heterochromatin studies is a growing need in maize breeding research, since knob features are associated with considerable variations in morphological types and yield. Such studies provide quick and easy method of screening the genotypes facilitating the assessment of the genetic variation among those features in the
prevailing climatic conditions. Of course the characterization of knobs would be helpful in selecting specific knob combination for further basic and applied studies and thus the new combinations could be obtained by crossing specific groups. Simultaneously knob polymorphism might be exploited in a controlled, reproducible and predictable fashion to derive inbreds for hybrid production because good hybrids require several linkage groups heterozygous for knobs for superior growth and development. Possibly the implication of geographical pattern would raise the issue of possible associations between the knob forming sites and agronomic adaptation.

REFERENCES