Theor Appl Genet (1994) 88:557–560

D. P. Biradar · D. G. Bullock · A. Lane Rayburn

Nuclear DNA amount, growth, and yield parameters in maize

Received: 9 April 1993 / Accepted: 12 October 1993

Abstract Extensive nuclear DNA content variation has been observed in *Zea mays*. Of particular interest is the effect of this variation on the agronomic potential of maize. In the present study, yield and growth data were collected on 12 southwestern US maize open-pollinated populations. These populations, originally cultivated by the Indians of the southwestern US for both human and animal consumption and adapted to various altitudes, were grown in replicated plots at the University of Illinois Agronomy-Plant Pathology South Farm. All growth and yield parameters were found to be negatively correlated with nuclear DNA amount. The negative correlations of nuclear DNA amount and growth parameters were more pronounced at 60 days after planting (DAP) than 30 DAP. Agronomically-important yield parameters, such as ear or seed weight and seed number per plant, also exhibited a significant negative correlations with nuclear DNA amount. These correlations demonstrate how the nucleotype may exhibit a high degree of influence on the agronomic phenotype. Although the results presented here represent only three replications at one location in 1 year, the observations noted suggest that nucleotype plays an integral role in determining the agronomic performance of maize. Further studies are needed to fully document this role.

Key words *Zea mays* L. · Genome size · Adaptation · Nucleotype · Agronomic performance

Introduction

Maize (*Zea mays* L.) has shown significant variation in genome size (Laurie and Bennett 1985; Rayburn et al. 1985; Rayburn 1990; Rayburn and Auger 1990a, b) which has been correlated with latitude, altitude, and potential maturity. Genome size was negatively correlated with latitude (Laurie and Bennett 1985; Rayburn et al. 1985). The relationship between genome size and altitude of adaptation was more complex. DNA amount decreases either with an increase or decrease from an altitude of about 1 500 m in the populations observed by Rayburn (1990) and Rayburn and Auger (1990b). It appears that smaller genome sizes of low- and high-altitude maize may be a result of adaptation to specific environmental conditions. In the same maize lines Bullock and Rayburn (1991) observed that, regardless of the altitude of adaptation, the length of growing season was correlated with genome size. The lines used in the altitude studies were southwestern Indian maize lines. These lines were selected from various altitudes by the southwestern US Indians for producing food and fodder. Thus, indications are that selection for agronomic performance at specific altitudes may be correlated with genome size.

There are many studies where nuclear DNA contents have been correlated with cellular parameters like nuclear volume, cell volume, mitotic cycle time, duration of meiosis, and chloroplast number per guard cell (Van't Hof and Sparrow 1963; Bennett 1971; Evans and Rees 1971; Price 1976; Cavalier-Smith 1978; Butterfass 1983; Ho and Rayburn 1991). The effects on such different cellular parameters due to nuclear DNA contents are referred to as nucleotypic effects. The term nucleotype was first defined by Bennett (1972). Nucleotypic effects are not restricted to the cellular level. The rates of development and the amount of growth at the cellular level also determine the rate of development and amount of growth of the whole plant. In higher plants, the nucleotypic effects are additive at successive cell cycles so that they could have a major impact on parameters of agronomic importance, e.g., growth rate and seed weight (Bennett 1987). Since such parameters determine the agronomic yield of any crop, it is pertinent to identify the effect

---

Communicated by J. W. Snape

D. P. Biradar · D. G. Bullock · A. Lane Rayburn (✉)
Agronomy Department, University of Illinois, 320 Plant and Animal Biotechnology Laboratory, 1201 W. Gregory, Urbana, IL 61801, USA

of a particular genome size on its growth and yield components. As suggested by Bennett (1976), genome size adaptation may be implicated in agriculture and plant breeding and thus should be investigated. In his study, Bennett (1976) dealt specifically with factors correlated with DNA variation at an interspecific level. Factors associated with DNA amounts at an intraspecific level may be different. No study to-date has attempted to explore the relationship between intraspecific genome size variation and agronomic performance in a major crop species. Studies have correlated genome size and cellular parameters and thus have inferred an effect on agronomic importance. However, no study has been performed under natural field conditions. Total yield in a crop is a function of different growth and yield components, any correlation of genome size with growth and yield components will ultimately reflect a correlation of genome size on the final yield of maize.

The objective of this study was to determine how growth and yield parameters are correlated with genome size and to provide evidence of the relationship between genome size and growth and yield parameters in maize under field conditions.

Materials and methods

The maize lines used in this study are open-pollinated southwestern US Indian maize populations that were obtained from the North Central Regional Plant Introduction Station at Ames, Iowa. They were selected as types typically grown and initially collected at the elevations indicated (Table 1). Twelve maize lines were selected based on the reported genome sizes by Rayburn (1990) and Rayburn and Auger (1990b). The lines used in this study were collected within the states of Arizona (AZ) and New Mexico (NM).

The study was carried out at the University of Illinois Agronomy-Plant Pathology South Farm at Urbana, Ill., in 1992. Planting was done on 13 May with a tractor-drawn mechanical planter. Each plot was 2.3 m wide (three rows) by 7.7 m long. The experimental design was a randomized complete block with three replications. All plots received common agronomic practices during the experimental period. For all growth and yield parameter measurements, five randomly-selected competitive plants from the central row were used and means were calculated for correlation analysis.

The growth parameters, plant height, number of leaves, and leaf area, were recorded at 30 and 60 days after planting (DAP). Plant height was measured as the distance from the soil surface to the base of the whorl. Only leaves with a visible collar were used for determining the number of leaves at both 30 and 60 DAP. Leaf area at 30 DAP was calculated by measuring the length and width of each leaf and then multiplying by a factor 0.75 (Montgomery 1911). At 60 DAP, the fourth fully-opened leaf from the top was used to measure the length and width and it was multiplied by the number of leaves and a factor 0.75 to calculate the leaf area. Yield parameters were recorded on the same five plants that were used for measuring the growth observations. Ears from the five plants were harvested, air-dried for 2 days, and then oven-dried at 65 °C for 3 days to a constant dry weight. The yield parameters, ear weight, seed weight, number of seeds, and test weight of 100 seeds, were also recorded at harvest.

Correlation coefficients were calculated with the Proc Corr procedure of SAS (SAS 1985) by using the reported genome sizes of AZ and NM lines with their respective growth and yield parameters.

Results and discussion

The lines used in this study were originally collected from different altitudes in the southwestern US states of AZ and NM and had a wide variation in genome size (Table 1). Since these lines represent open-pollinated populations, variability with respect to genome size did exist (Rayburn 1990; Rayburn and Auger 1990b). However, this variability did not preclude significant differences among the populations. In another independent study in which the genome size of several of these populations was re-examined, genome sizes were found to be very close to the original DNA content determinations (Ho and Rayburn 1991).

Yield parameters of the maize populations studied are presented in Table 2. Correlation coefficients were then calculated between genome size and parameters of

Table 1 Southwestern US Indian maize lines with their altitude of collection and genome size

PI number[a]	State-altitude (m)[b] of original collection	Genome size[c] (arbitrary units)
218134	NM-2 090	112.2
218141	NM-1 850	126.1
218142	NM-2 150	117.0
218144	NM-1 530	136.5
218158	NM-1 850	136.9
218161	AZ-1 630	123.2
218174	AZ-1 300	129.7
218175	AZ-1 300	127.5
218177	AZ-1 300	132.4
218179	AZ-700	117.2
218187	AZ-92	115.5
218189	AZ-30	111.4

[a] North Central Plant Introduction Station accession number

[b] State: AZ (Arizona), NM (New Mexico); altitude: m (meters)

[c] NM genome size data from Rayburn (1990) and AZ genome size data from Rayburn and Auger (1990b)

Table 2 Maize lines with their yield parameters

Lines	Cob weight (g/plant)	Seed weight (g/plant)	Weight of 100 seeds (g)	Seed number per plant
PI218134	98.5	86.1	20.2	427
PI218141	104.1	90.7	28.6	317
PI218142	54.7	43.5	22.0	198
PI218144	34.5	24.7	19.5	127
PI218158	71.9	51.3	16.8	306
PI218161	54.4	47.4	21.1	225
PI218174	51.7	43.4	14.5	300
PI218175	91.3	78.7	22.1	356
PI218177	27.1	18.6	24.7	75
PI218179	72.4	62.8	19.3	326
PI218187	98.5	87.8	18.6	471
PI218189	132.1	106.9	26.5	403
Standard error of means	13.1	11.2	1.6	48

growth and yield (Table 3). The results indicate a general negative correlation of genome size with growth and yield parameters in maize.

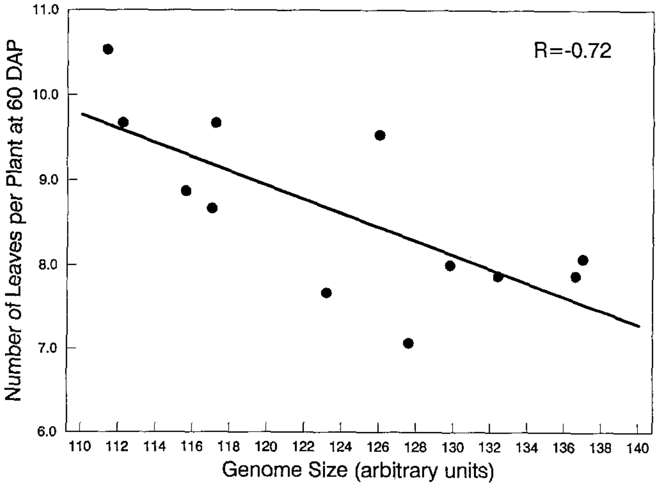
Genome-size effects on different cellular parameters are well documented in the literature and it has been hypothesized that the effects are additive in nature and extend to multicellular structures (Bennett 1987). Plant size is mainly determined by cell number and cell size. The rate of cell division has been hypothesized to be correlated with nuclear DNA amount: the greater the nuclear DNA amount, the longer the time required for replication (Van't Hof 1965).

Plant height, the number of leaves, and leaf area parameters, could all be affected by genome size at the cellular level. Such a correlation could result in plants with an increase in leaf number, plant height, and leaf area. A higher number of leaves, more height and leaf area would act to increase the photosynthetic source for the final sink (developing grain in maize). The correlation data suggest that the negative relation of growth parameters with genome size was more pronounced at 60 DAP (Table 3; Figure 1) compared to 30 DAP. The negative correlation of genome size and plant height seen in this study is contrary to the observations of Lawrence (1985) in *Senecio* species. Therefore, more conclusive evidence is needed to support the hypothesis that nucleotypic effects on cell division are responsible for the correlation between genome size and plant size parameters in maize.

Table 3 Correlation coefficients of genome size with growth and yield parameters

Parameter	R-value	*P*-value
Plant height-30 DAP	−0.14	0.65
Plant height-60 DAP	−0.60	0.04
Number of leaves-30 DAP	−0.46	0.13
Number of leaves-60 DAP	−0.72	0.008
Leaf area-30 DAP	−0.55	0.06
Leaf area-60 DAP	−0.54	0.07
Ear weight/plant	−0.63	0.03
Seed weight/plant	−0.67	0.02
Weight of 100 seeds	−0.23	0.46
Number of seeds/plant	−0.56	0.06

Fig. 1 Relationship of genome size to number of leaves per plant at 60 days after planting. Genome-size data expressed as arbitrary units taken from Rayburn 1990 and Rayburn and Auger 1990b. R value significant at $\alpha = 0.01$



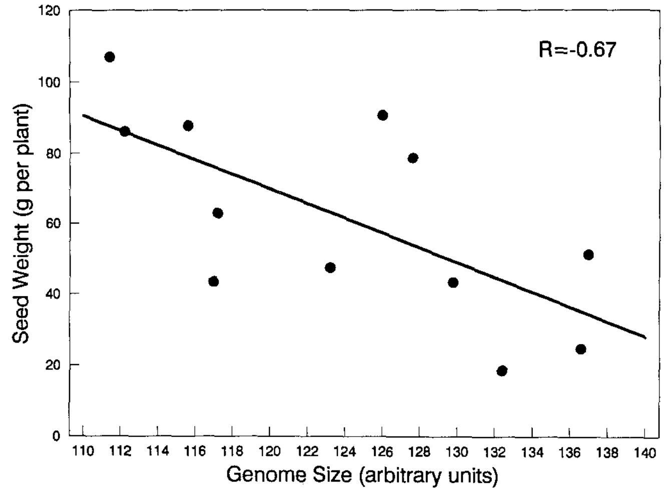


Fig. 2 Relationship of genome size to seed weight per plant. Genome size data expressed as arbitrary units taken from Rayburn 1990 and Rayburn and Augar 1990b. R value significant at $\alpha = 0.05$

In maize a relationship exists between plant size and yield. Rayburn et al. (1985) hypothesized that as maize migrated northward from Mexico into the northern US, simultaneous selection for early maturation and maximum plant size occurred. Such selection appeared to lower nuclear DNA amounts. Bennett (1976) observed a relationship between crop plant distribution and genome size. In the southwestern US maize lines examined in the present study, the lines with lower DNA amounts were adapted to shorter growing seasons (Bullock and Rayburn 1991). When grown at the Agronomy-Plant Pathology South Farm at Urbana, Ill., all the lines flowered within a 2-week period between $2\frac{1}{2}$ months to 3 months after planting. Whether the flowering times among these southwestern maize lines reflect the flowering times in the original adapted areas or resulted from growing the lines at Urbana is unknown. However, weather conditions during this growing season resulted in no stress on the plants at any time during growth. The temperatures were unusually mild with high temperatures around 25–26 °C and low temperatures approximately 14–15 °C during much of the growing season. Therefore, no heat stress was present. In addition, the lines were fully matured before any threat of frost. With respect to precipitation, the total amount during the growing season was about 58 cm. This amount was more than adequate for maize growth and development; no drought stress occurred. Therefore the yield results presented would represent maximum yields that these plants would have in an unstressed environment at Urbana. Whether these numbers reflect the true yield at the adapted locations is unknown. However, it is apparent from the results that, at this location, genome size and yield parameters are negatively correlated (Table 3; Figure 2). Whether or not this correlation holds in the adapted region has yet to be determined. This does not, however, negate the observed correlation between yield and genome size.

The yield of a maize plant is dependent on many components, such as the number of ears, ear or seed weight, the number of seeds per ear, and test weight. Yield or yield components in most crops are manifestations of their growth components. All the yield parameters in this study were negatively correlated with genome size. A similar negative association of genome size and potential yield parameters, such as seed weight, were observed in *Senecio* species (Lawrence 1985). In contrast, Bennett (1972) reported significant positive relationships between DNA amount and seed weight in *Allium* and *Vicia*. Such positive relations were also seen in *Crepis* (Jones and Brown 1976) and in certain British legumes and grasses (Mowforth 1985). Similar correlations are not expected in all species (Cavallini and Natali 1991) because of the parallel effects of genome size on different phenotypic characters (Bennett 1987) or environmental conditions. Grime (1983) pointed out that one should consider other plant attributes, additional to those associated with DNA content, which control relative growth rate. However, under the special conditions observed in the study reported here, genome size appears to have an usually high degree of control over growth and yield parameters.

The role of nucleotype is becoming increasingly important with so many studies establishing a definite and conclusive relationship of genome size to the geographical distribution of plants. As in an interspecific study of Bennett (1976), there appeared to be a correlation between adaptation and genome size. However, the results of the present study indicate an opposite correlation to that observed by Bennett (1976). Laurie and Bennett (1985), as well as Rayburn et al. (1985), revealed a pattern similar to that seen in the present study. It should be noted that all the above intraspecific studies were in maize. Studies are needed in different crops to determine the relationship of genome size with growth and yield parameters under field conditions. The present study, although limited to one location in 1 year, showed definite trends between the nucleotype and agronomic performance. More field experiments are needed as nucleotype is assessed over multiple environments. As proposed by Bennett (1972) due consideration must be given to the role of nucleotype in the determination of phenotype and, as such, to the growth and yield of crop species.

References

Bennett MD (1971) The duration of meiosis. Proc R Soc Lond B 178: 227–299

Bennett MD (1972) Nuclear DNA content and minimum generation time in herbaceous plants. Proc R Soc Lond B 181:109–135

Bennett MD (1976) DNA amount, latitude, and crop plant distribution. Envir Exp Bot 16:93–108

Bennett MD (1987) Variation in genomic form in plants and its ecological implications. New Phytol 106:177–200

Bullock DG, Rayburn AL (1991) Genome size variation in southwestern US Indian maize populations may be a function of effective growing season. Maydica 36:247–250

Butterfass T (1983) A nucleotypic control of chloroplast reproduction. Protoplasma 118:71–74

Cavalier-smith T (1978) Nuclear volume control by nucleoskeletal DNA, selection for cell volume and cell growth rate and the solution of the DNA C-value paradox. J Cell Sci 34: 247–278

Cavallini A, Natali L (1991) Intraspecific variation of nuclear DNA content in plant species. Caryologia 44:93–107

Evans GM, Rees H (1971) Mitotic cycles in dicotyledons and monocotyledons. Nature 233:350–351

Grime JP (1983) Prediction of weed and crop response to climate based upon measurements of nuclear DNA content. Aspects Appl Biol 4:87–98

Ho I, Rayburn AL (1991) The relationship between chloroplast number and genome size in *Zea mays* ssp. *mays*. Plant Sci 74: 255–260

Jones RN, Brown LM (1976) Chromosome evolution and DNA variation in *Crepis*. Heredity 36:91–104

Laurie DA, Bennett MD (1985) Nuclear DNA content in the genera *Zea* and *Sorghum*. Intergeneric, interspecific and intraspecific variation. Heredity 55:307–313

Lawrence ME (1985) *Senecio* L. (Asteraceae) in Australia: nuclear DNA amounts. Aust J Bot 33:221–232

Montgomery EG (1911) Correlation studies in corn. Nebraska Agric Exp Stn Annu Rep 24:108–159

Mowforth MAG (1985) Variation in nuclear DNA amounts in flowering plants: an ecological analysis. PhD thesis, University of Sheffield, UK

Price HJ (1976) Evolution of DNA content in higher plants. Bot Rev 42:27–52

Rayburn AL (1990) Genome size variation in southwestern US Indian maize adapted to various altitudes. Evol Trends Plants 4: 53–57

Rayburn AL, Auger JA (1990a) DNA content variation in the ancient indigenous races of Mexican maize. Acta Bot Neerl 39: 197–202

Rayburn AL, Auger JA (1990b) Genome size variation in *Zea mays* ssp. *mays* adapted to different altitudes. Theor Appl Genet 79: 470–474

Rayburn AL, Price HJ, Smith JD, Gold JR (1985) C-based heterochromatin and DNA content in *Zea mays*. Am J Bot 72: 1610–1617

SAS Institute (1985) SAS user's guide: statistics, version 5. SAS Institute Cary, North Carolina, USA

Van't hof J (1965) Relationships between mitotic cycle duration, S-period duration and the average rate of DNA synthesis in the root meristem of several plants. Exp Cell Res 39:48–58

Van't hof J, Sparrow AH (1963) A relationship between DNA content, nuclear volume and minimum mitotic cycle time. Proc Natl Acad Sci USA 49:897–902