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Final Report to
City of Boulder Open Space and Mountain Parks Research/Monitoring Program

Population Dynamics of Big Bluestem (*Andropogon gerardii)* in Boulder Open Space

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ABSTRACT

Big bluestem populations in the Boulder Open Space contain relatively even numbers of the two chromosome forms of the species (60 and 90 chromosomes). However, 90 chromosome plants are significantly larger in diameter and produce more flowers and seed biomass and have taller flowering stalks and longer leaves than 60 chromosome plants. The analysis of the amount of fertile seed produced is still being analyzed but appears to be about the same between the two. Looking at the populations for individual plant size, most individuals more than 10 cm. across flowered in 1995, but the minority produced any viable seed. The size distribution of individuals in 3 of the 4 sites studied are consistent with a healthy species that is currently reproducing successfully. The fifth (top of Davidson Mesa) consisted mainly of quite large individuals which suggests poor seed recruitment in recent years.

1. Objectives and Hypothesis

Big bluestem, *Andropogon gerardii* Vitman, was the dominant grass of the tallgrass prairie ecosystem (Weaver 1954) and forms an integral part of open habitats in the Boulder Open Space and Mountain Park system (Bock et al. 1995a,b). In the central Great Plains, it is impossible to determine fitness and reproductive success on a per-plant basis, because the species is so successful its impossible to tell where one plant ends and the next begins. In many locations in the Boulder Open Space, plants are sufficiently isolated that individual plants can be distinguished.

Objective 1: An important but poorly understood aspect of big bluestem biology is that populations west of the Missouri River contain high proportions of 90-chromosome (enneaploid, with 9 copies of the basic genome) plants, in addition to the more widespread 60 chromosome (hexaploid, 6 copies of the genome) plants. These two cytotypes are intermixed and interbreed (Keeler et al. 1987, Keeler 1990, 1992, Norrmann, Quarin and Keeler in prep.). Understanding whether this variation in polyploidy represents an adaptive polymorphism or a maladaptive genetic anomaly or something in between requires comparing the fitness of the two cytotypes, which, as indicated above, is feasible in Boulder Open Space, but not in tallgrass prairies farther east.

The null hypothesis was that in all populations both cytotypes have the same fitness: are the same size, have the same number of flowers and seeds.

Objective 2: Since plants of big bluestem have never been studied as individuals in natural populations, nothing is known of the size structure and age distribution. The ability to distinguish individuals in the Boulder Open Space allows looking and the size distribution and estimating an age distribution. This is the first such information for a native big bluestem population. The distributions found can be compared to expectations borrowed from other plant species that there should be many more small individuals than large, and a pyramidal distribution of sizes, as in a forest, with only a few very large trees, but many saplings.

The null hypothesis is that all sites are healthy and have many more small plants than large ones.

Methods

Four plots 10 x 10 m. plots were established in 1995. In each case the site was located based on one of Jane and Carl Bock's permanent stakes. The numbers given the

plot refer to the Bock plots, since this provides: 1) ease of relocation and 2) a coordinated and growing data base about that site. The plots of 1995 are: plot 36 (South Boulder Creek). This plot has the Bock Stake as its southwest corner. Plot 45 is along the Church Wildlife Transect, with Bock Stake 45 at the 4th meter from the S corner, on the east edge of the 10x10 m. plot. (Plot shifted north to avoid an area devoid of big bluestem). Plot 52 (Davidson Mesa) was established 1 m. w and 1 n of the fence that demarks the pasture containing Bock Stake 52 (there was not a satisfactory population of big bluestem adjacent to Stake 52). Plot 58 is in the Sans Souci Trailer Park Grazing Exclosure, the southwest corner of the plot 5 m. w and 5 s of Bock Stake 58. (Again, the area immediately next to the stake lacked big bluestem.)

Table 2. Description of Plots Studied

Plot	Location	History	Description
36	South Boulder Creek	grazed Nov-Feb	low, wet
45	Church Wildlife Transect	grazed Jan-May	gravely, sub-irrigated
52	Davidson Mesa	grazed Jan-May	xeric, top of mesa
58	Sans Souci Mobile Home Park	ungrazed	low, wet

These plots represent a variety of land uses, ungrazed to winter grazed, because the goal was to understand big bluestem biology. Since the species is very responsive to landuse, the diverse plots mean that any pattern seen across them is big bluestem- not landuse- specific.

Plots were established to be close to the Bock Stakes but include at least 25 plants of big bluestem. They were located with a compass and meter stick to run with the ordinal directions for ease of relocation.

Once the plot were established, all big bluestem plants within them were mapped to the nearest cm. on graph paper. Four metersticks held together with carpenter's corners aided in this, but the accuracy is probably only +/- 5 cm. due to 1) problems getting the quadrat level in deep vegetation, 2) the thickness of the metersticks creating an error and 3) accumulated small errors of angle.

Plants drawn on the map were numbered and the following recorded: size (as the longest diameter and a diameter at right angles to that), height of tallest flowering stalk, number of flowering stalks, number of inflorescence branches (the "feet" of turkeyfoot), weight of seeds produced, length of longest leaf, leaf, stigma and anther color. Seed number and number of filled seeds will be determined. I hope to locate a mapping computer program and more accurately determine plant areas. Analysis of plant color markers and number of filled seeds is incomplete at this time.

I determined "a plant" from the following information: first, more than 15 cm. from another clump of big bluestem. This was supplemented with observations on flower and foliage color, shape and size. In Plot 52 I tested my judgment that two clones run together (Plot 52 map, plants 25 and 26. The apparent gap between them is in fact filled by a cow pie. Plants 7 and 35, plants 17 and 18, plants 28 and 32, and plants 5 and 33. In three of these cases I a found quite different DNA values. For 28 and 32 the DNA values are 8.6 and 8.0 respectively, and for 5 and 33 5.5 and 5.93. Since in Plot 36 two plants that on later inspection I decided were the same individual were analyzed independently: both plant 10 and plant 21 had 9.23 picograms of DNA, these values suggest, but do not

establish that they are different individuals. The net result is that I am generally confident about the decisions about where one plant ends and the other begins.

At least 20 plants per plot were cytotyped: a leaf about 5 cm. long was picked fresh, placed in a plastic bag with a piece of wet paper toweling and a label, and sent by Federal Express to Dr. Arumuganathan of the Flow Cytometry Laboratory, University of Nebraska Lincoln. Dr. Arumuganathan determined the amount of nuclear DNA per leaf (e.g. Keeler et al. 1987). Since nuclear DNA is correlated to chromosome number the chromosome number can be inferred from nuclear DNA contents. (One revision from the published work is that the "high DNA" cytotypes have 90 chromosomes, not 80 as I previously published. Paper in preparation: Norrmann, Quarin and Keeler). For Plot 52 every plant fully within the plot was cytotyped. For Plot 45, on the other extreme, only 8.6% (22 of the 257 within the plot boundaries) were cytotyped. (A set of samples from plot 45 sent in late September produced peculiar results so those will be redone in 1996). Where only a sample of the plants in the plot were cytotyped, the plants were chosen to represent a variety of sizes and to minimize the chance of sampling one diffuse clone repeatedly.

Statistical analysis was carried out using the Statview Program (Abacus Concepts Inc. Berkeley CA, 1995 edition).

Results

The 60 and 90 chromosome cytotypes were about equally common in all plots (Table 2). About 5% of the plants seen appear to have intermediate chromosome numbers and are probably aneuploid, based on the cytological studies of big bluestem done by G.A. Norrmann and C.A. Quarin.

Table 2. Distribution of Big Bluestem Cytotypes in Boulder Open Space

Bock Plot No.	Number (%) 60 chromosomes	Number (%) 90	Number (%) Other values	Total Plants Cytotyped	Total No. Plants in 100 sq. meters
36	9 (41)	13 (59)	0	22	110
45	12 (48)	11 (44)	2 (8)	25	304
52	15 (60)	9 (36)	1 (4)	25	36
58	12 (57)	7 (33)	2 (10)	21	32
Tot.	48 (52)	40 (43)	5 (5)	93	483

High DNA (enneaploid) clones were significantly larger than low DNA (hexaploids) (Table 3).

Table 3. Comparisons of Size by Cytotype

Size was estimated by multiplying longest diameter by diameter at right angles) M-W U (Z) is the Mann-Whitney nonparametric U test for difference, Z being the numerical value produced.

Plot	Size								
	60 chromosomes			90 chromosomes			statistics		
	mean	std. dev.	N	mean	std. dev.	N	M-W U(Z)	p	
36	1352.79	1048.40	9	2058.64	2073.02	11	-0.27	.7903	ns
45	301.36	505.29	11	7193.82	5165.12	10	-3.25	.0012	***
52	9363.82	11903.56	17	16257.14	7429.41	17	-1.94	.0527	ns
58	5845.17	8983.35	13	5787.50	7112.45	5	-0.58	.5623	ns
Total	3727.08	6858.11	36	7325.06	7232.00	31	-2.78	0.005	**

High DNA plants also produced significantly more flower stalks on a per-plant basis (Table 4). High DNA plants also produced significantly more inflorescence branches per plant (Table 5) and more importantly significantly more seeds (Table 6).

Table 4. Comparisons of Number of Flowering Stalks per Plant by Cytotype

M-W U (Z) is the Mann-Whitney nonparametric U test for difference, Z being the numerical value produced

Plot	No. Flowering Stalks								
	60 chromosomes			90 chromosomes			statistics		
	mean	std. dev.	N.	mean	std. dev.	N	M-W U(Z)	p	
36	8.78	15.8	9	3.36	13.66	11	-1.254	.2100	ns
45	5.18	11.70	11	47.50	15.99	10	-3.66	.0002	***
52	11.75	19.52	16	22.43	10.78	7	-2.27	.0231	*
Total	9.00	16.24	36	22.43?	22.18	30	-2.92	.0035	**

Table 5. Comparisons of Number of Inflorescence Branches by Cytotype

M-W U (Z) is the Mann-Whitney nonparametric U test for difference, Z being the numerical value produced

Plot	No. of Inflorescence Branches								
	60 chromosomes			90 chromosomes			statistics		
	mean	std. dev.	N.	mean	std. dev.	N	M-W U(Z)	p	
36	33.33	53.64	9	14.73	11.25	11	-1.90	.8494	ns
45	33.09	93.64	11	351.40	225.34	10	-3.25	.0004	***
52	26.47	50.58	17	60.14	35.14	7	-2.51	.0121	**
Total	30.11	64.99	37	136.80	200.59	30	-3.80	.0001	**

Table 6. Comparison of Seed Weight per Plant by Cytotype

M-W U (Z) is the Mann-Whitney nonparametric U test for difference, Z being the numerical value produced

Plot	Seed Weight per Plant (grams)								
	60 chromosomes			90 chromosomes			statistics		
	mean	std. dev.	N.	mean	std. dev.	N	M-W U(Z)	p	
36	0.949	1.330	9?	0.565	0.450	?	-0.038	.9697	ns
45	0.765	1.933	11	13.85	10.02	11	-3.35	.0008	***
52	.00008	<.0001	17	.00016	<.0001	7	-1.93	.0527	ns
ALL	0.789	1.56	37	5.604	8.532	31	-3.99	<.0001	***

When compared on a per-square meter basis, the differences are much less: number of flowering stalks does not differ on a per-area basis (Table 8), number of inflorescence branches per square meter differed but not significantly (low DNA mean 0.031 (sd 0.056, n=37), high DNA mean 0.044 (sd 0.096, n=30) (Mann-Whitney Z=-1.93, p=0.053) and seed weight per square meter is only slightly greater (p=0.02, Table 9) for high DNA plants. This suggests there is slightly greater reproduction by high DNA plants but that most of the effect is due to the fact that they are larger clones.

Table 7. Comparison of Number of Flower Stalks per sq. meter, by Cytotype

Flower Stalks/sq. cm. was estimated by dividing total flower stalks (Table 5) by Size (Table 4), on a per-plant basis. M-W U (Z) is the Mann-Whitney nonparametric U test for difference, Z being the numerical value produced.

Plot	No. Flowering Stalks/ square meter								
	60 chromosomes			90 chromosomes			statistics		
	mean	std. dev.	N	mean	std. dev.	N	M-W U(Z)	p	
36	.944	1.61	9	.336	.425	11	-1.71	.0874	ns
45	1.74	2.40	11	1.06	1.33	10	-0.70	.9439	ns
52	0.199	.251		0.177	.063	7	-.535	.593	ns
ALL	0.876	1.62	35	0.521	0.882	30	-.211	.8332	ns

Table 8. Comparison of Seed Weight per Square Meter to Cytotype

Seed weight (table 6) divided by plant size (table 3)
M-W U (Z) is the Mann-Whitney nonparametric U test for difference, Z being the numerical value produced

Plot	Seed Weight/ sq. meter								
	60 chromosomes			90 chromosomes			statistics		
	mean	std. dev.	N.	mean	std. dev.	N	M-W U(Z)	p	
36	.158	.308	9	.127	.039	11	-.342	.7324	ns
45	.201	.296	11	.293	.401	11	-.985	.325	ns
52	.009	.012	17	.016	.012	11	-1.94	.0509	ns
All	.104	.234	36	.153	.286	31	-2.27	.0236	*

Some of this is explained by seed weight per flower stalk, which was highly significantly different (low mean = 0.087 (sd=0.065, n=27), high mean = 0.224

(sd=0.182, n=28), Mann-Whitney Z=-3.48, p= 0.0005). The high DNA plants produced more seed biomass per flowering stalk.

Analysis of number of filled seeds by plant is in progress, but requires 20-30 minutes per plant and may not be complete until well into January. Results for the first plot completed indicate as expected from biomass, more capsules are produced by high DNA plants, and but, as expected from studies of meiosis, fewer of these contain viable seeds. I am not able to determine loss to insects, so many variables are included in these results.

Two other measures were made because data in Kansas and Nebraska showed high DNA plants to be consistently (but not always statistically significantly) larger than low DNA plants. That is confirmed here: the longest leaf (Table 9) and height of tallest flowering stalk (Table 10) are both significantly greater in high DNA plants than low DNA plants.

Table 9. Comparison of Length of Longest Leaf per Plant by Cytotype

M-W U (Z) is the Mann-Whitney nonparametric U test for difference, Z being the numerical value produced

Plot	Longest Leaf (cm)								
	60 chromosomes			90 chromosomes			statistics		
	mean	std. dev.	N	mean	std. dev.	N	M-W U(Z)	p	
36	41.11	11.11	9	47.80	5.51	10	-1.18	.2364	ns
45	27.64	7.58	11	33.10	4.36	10	-1.94	.0528	ns
52	25.24	5.15	17	31.57	4.61	7	-2.47	.0133	**
All	29.95	10.08	37	37.86	8.87	28	-3.46	.0005	**

Table 10. Comparison of Height of Flowering Stalks by Cytotype

Tallest 3 flowering stalks were measured; tallest one is used here.
M-W U (Z) is the Mann-Whitney nonparametric U test for difference, Z being the numerical value produced

Plot	Flowering Stalk Height (cm)								
	60 chromosomes			90 chromosomes			statistics		
	mean	std. dev.	N	mean	std. dev.	N	M-W U(Z)	p	
36	84.22	29.62	9	88.73	35.95	11	-0.49	.6214	ns
45	45.91	45.02	11	118.80	14.42	10	-3.25	.0009	***
52	48.12	38.69	17	87.00	13.09	7	-2.29	.0222	*
All	56.24	41.02	37	94.43	33.53	30	-3.93	<.0001	**

The many significant patterns in Tables 2-7 (above) can be seen as a function of plant size, since plant size is statistically significantly correlated with number of flower stalks, number of inflorescence branches and seed weight in all plots.

Table 11. Correlations to Plant Size
All values are statistically significant at the 0.001 level

Plot	Number of Flower Stalks	No. Inflorescence Branches	Seed Weight
36	.559	.561	.537
45	.825	.746	.841
52	.736	.599	.712
58	not applicable		

Analysis of the seeds collected to determine what proportion of the capsules contain a filled seed is complete only for Plot 52. For Plot 52, 60 chromosome plants averaged 8.7 filled seeds per plant (sd=18.4, N=15), while 90 chromosome plants averaged 3.1 filled seeds per plant (sd=8.3, N=7), a difference that is not significant (Mann-Whitney U Test, Z=-0.881, p= 0.378).

The plant sizes ranged from very tiny (a single shoot) to plants greater than 2 m. in diameter (Table 13).

Table 13. Distribution of Sizes

Plot	Maximum Diameter in cm. (%)							
Name	0-9	10-49	50-99	100-149	150-199	200-249	250-299	#
36	22 (20)	56 (51)	25 (23)	4 (4)	3 (3)	0	0	110
45	112 (37)	126 (41)	17 (6)	35 (12)	12 (4)	2 (1)	0	304
52	1 (5)	5 (14)	8 (22)	14 (39)	4 (11)	4 (11)	0	36
58	6 (19)	6 (19)	8 (25)	7 (21)	2 (6)	2 (6)	1 (3)	32
Tot.	141 (29)	193 (40)	58 (12)	60 (12)	21 (4)	8 (2)	1	482

This data (Table 12) indicates that most sites have a size distribution that would be considered "healthy", for example Plot 45. It has many small plants, decreasing in size up to a few very large plants. (Although a single year study cannot demonstrate that the small plants are young plants and not dying segments of old clones, this seems unlikely. See the distribution of small plants in the Plot Maps). The situation for at least Plot 52 is less comfortable: 60% of the plants are over 100 cm. in diameter and thus decades old. None of the populations appear to be in serious trouble, as would be indicated by the actual absence of smaller size classes.

The success of the 1995 study provides an opportunity to look at the interplay of big bluestem population structure and site history. Since big bluestem is virtually unknown in terms of population structure (in eastern tallgrass prairies it is impossible to separate individuals), not only does this have practical applications in the Open Space, it will be important to a general understanding of the dynamics of this economically and ecologically important species.

DISCUSSION

This study presents the first comparison on big bluestem cytotypes on an individual plant basis. All four populations in the Boulder Open Space that were studied had approximately equal numbers of 60 and 90 chromosome plants, with less than 5% of the plants having intermediate chromosome numbers, as determined by flow cytometry. This is very similar to the pattern at Konza Prairie, Manhattan KS, and Nine-Mile Prairie, Lincoln NE, and very distinct from prairie remnants east of the Missouri River, which contained 95% 60 chromosome plants (Keeler 1990). Also similar to Kansas was the 5% frequency of odd chromosome numbers, apparently aneuploids with unbalanced chromosome complements. When this project was initiated, it seemed reasonable to suppose that big bluestem populations in Boulder, on the western edge of the species' range would contain mostly 90 chromosome plants as the end of an east-west gradient, but that is not the case. Similarity to KS and NE prairies and differences from prairies farther east are not easily explained at this time.

The 90 chromosome plants are consistently larger in size than 60 chromosome plants (Table 3). This result is significant when the plots are combined, but only significant for Plot 45, although in Plot 36 and 52 the 90 chromosome plants are larger. Larger size could be due to more rapid growth, but is more likely due to being older. This study is the first look at the population dynamics of big bluestem, so it is difficult to interpret this result. It could mean that big bluestem 90 chromosome plants live longer than 60 chromosome plants so that they attain greater size or that germination conditions favored 90 chromosome plants so that even if survival was random, there were more 90 chromosome plants. This will be further considered below.

The 90 chromosome plants produced statistically significantly more flowering stalks, more inflorescence branches and more seeds than the 60 chromosome plants, dominating reproduction (Tables 4-7). Note that Plot 36, which was the one where 90 chromosome plants were not bigger, did not flower in 1995, and so cannot be included in this analysis.

The reproductive dominance by 90 chromosome plants is predominantly a function of their size, since when placed on a per square meter basis, flowering is much less different between the cytotypes, although 90 chromosome plants having significantly more seed per square meter (Table 7 and 8). More complex analysis of plant size, for example an estimate of area other than the product of two diameters, and measurement of plant density, might help interpret this result.

As seen in other prairies (Nebraska, Kansas, Keeler in prep.) 90 chromosome plants are taller and have longer leaves than 60 chromosome plants (Tables 9-10). This is often the case in polyploids, and is seen as a result of having more DNA in the nucleus, which requires a larger nucleus, which usually leads to a larger cell, etc. (Stebbins 1971).

Three of the plots studied had a complex size distribution with many small plants. That would suggest that they are reproducing effectively. Plot 52 is sufficiently short in small plants that there might be some problem with big bluestem maintenance there. However, that is a mesa-top plot which the Bocks classified as mixed rather than tallgrass prairie, so the management consequences of poor big bluestem success there are perhaps less serious than in tallgrass sites.

The actual interpretation of the health of the populations is much more difficult since it needs to include the interaction of the two cytotypes. 60 chromosome plants of big bluestem can set a high frequency of seed since meiosis is regular (Norrmann et al. in

prep.). I have rarely collected more than 10% filled seeds from any naturally occurring big bluestem, however, so realized seed set is not anywhere near potential, for reasons unexplained by the literature.

90 chromosome plants, on the other hand, make a large number of chromosomally defective gametes, as 45 chromosomes are pulled to each pole during meiosis. Since this is not well-regulated, some of the combinations may end up with 30 chromosomes, while others appear to function decently with an odd (aneuploid) number of chromosomes. In any event, the theoretical and realized fertility of 90 chromosome plants is much less than of 60's (Norrmann et al. in prep., Keeler unpublished data).

In mixed populations, as far as we know, 60 and 90 chromosome plants freely cross pollinate. This should decrease the fertility of 60 chromosome plants and raise the fertility of 90 chromosome plants, in comparison to their success in a pure population of their own chromosome number. Since the Boulder Open Space plots are mixed, this is the situation that is of concern here. The larger size of the 90 chromosome plants means the pollen cloud of the population is dominated by poor quality pollen from 90 chromosome plants. Seed set will be consequently reduced. Since nothing is known of big bluestem population dynamics, there is no way to estimate how many seeds are needed for one seedling to successfully germinate and survive the first year, but from other species it would seem to be dozens to hundreds (e.g. Stearns 1992). Yet for the first population for which seed production has been analyzed (Plot 52), there were an average of 15 (60 chromosome) and 7 (90 chromosome) live, healthy seeds per plant, out of seed production which averaged 162.8 seeds per plant (60 chromosomes) and 492.4 seeds per plant (90 chromosomes) or 0.8 grams of seed (60) and 8.5 grams of seed (90) on 9 (60) and 22 (90) flowering stalks per plant. If I call the populations half of each cytotype, then the Boulder Open Space big bluestem plants are averaging one healthy seed per 5 grams of seed biomass or one healthy seed per flowering stalk. That is not a very large seed rain: less than 1 seed per square meter. Since big bluestem seeds do not form a persistent seed bank (Glenn-Lewin et al. 1990), and 1995 was the second wettest year on record, this is a best-case scenario.

Interpreting these patterns for the health of big bluestem requires assuming that the conditions are stable and represent at least a temporary equilibrium. If that is assumed, then something odd is going on in Plot 45, since the 60 chromosome plants are very much smaller than the 90 chromosome plants. At present I am at a loss to explain that. Since statistically 90's are generally larger, the dynamics in these populations generally seem unbalanced: for it to be stable I'd expect equal numbers of small, medium and large 60 and 90 chromosome plants.

The reproductive results should not be taken too seriously however: since 1995 was a particularly wet year and wet years generally favor larger plants (which need more water to support their larger tissues), the 90 chromosome plants may have been especially fecund this year: a more normal year might balance the two better reproductively, but unfortunately, probably with fewer total seeds per area.

This one-summer study established permanent plots where big bluestem can be easily monitored in the future and provided the first look at the big bluestem population biology. It raised a number of interesting questions. Although there are a lot of issues that suggest problems for big bluestem in the Open Space, in fact the high density of plants (e.g. 0.4 to 2 per square meter, or something like 25% basal cover) suggests healthy populations.

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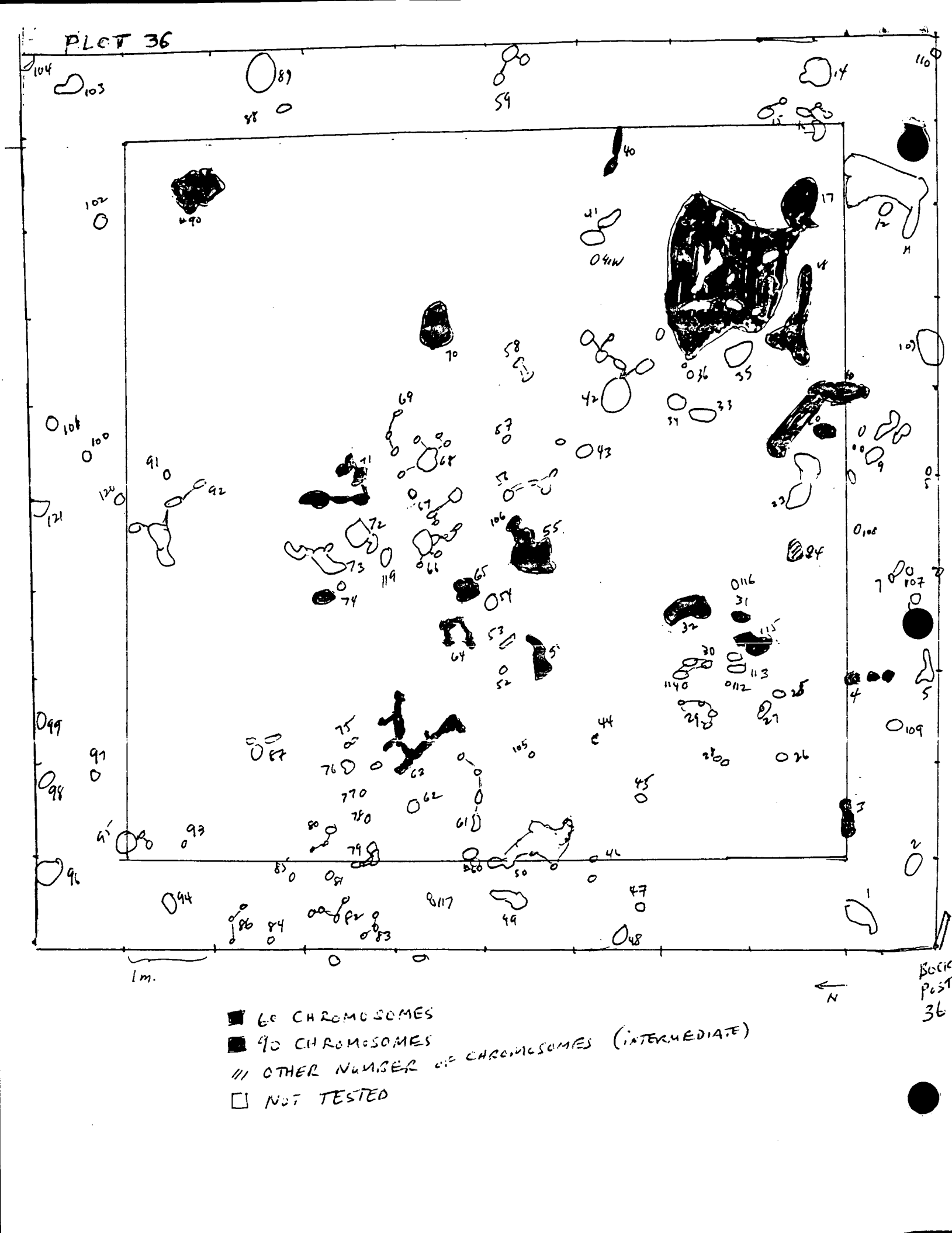
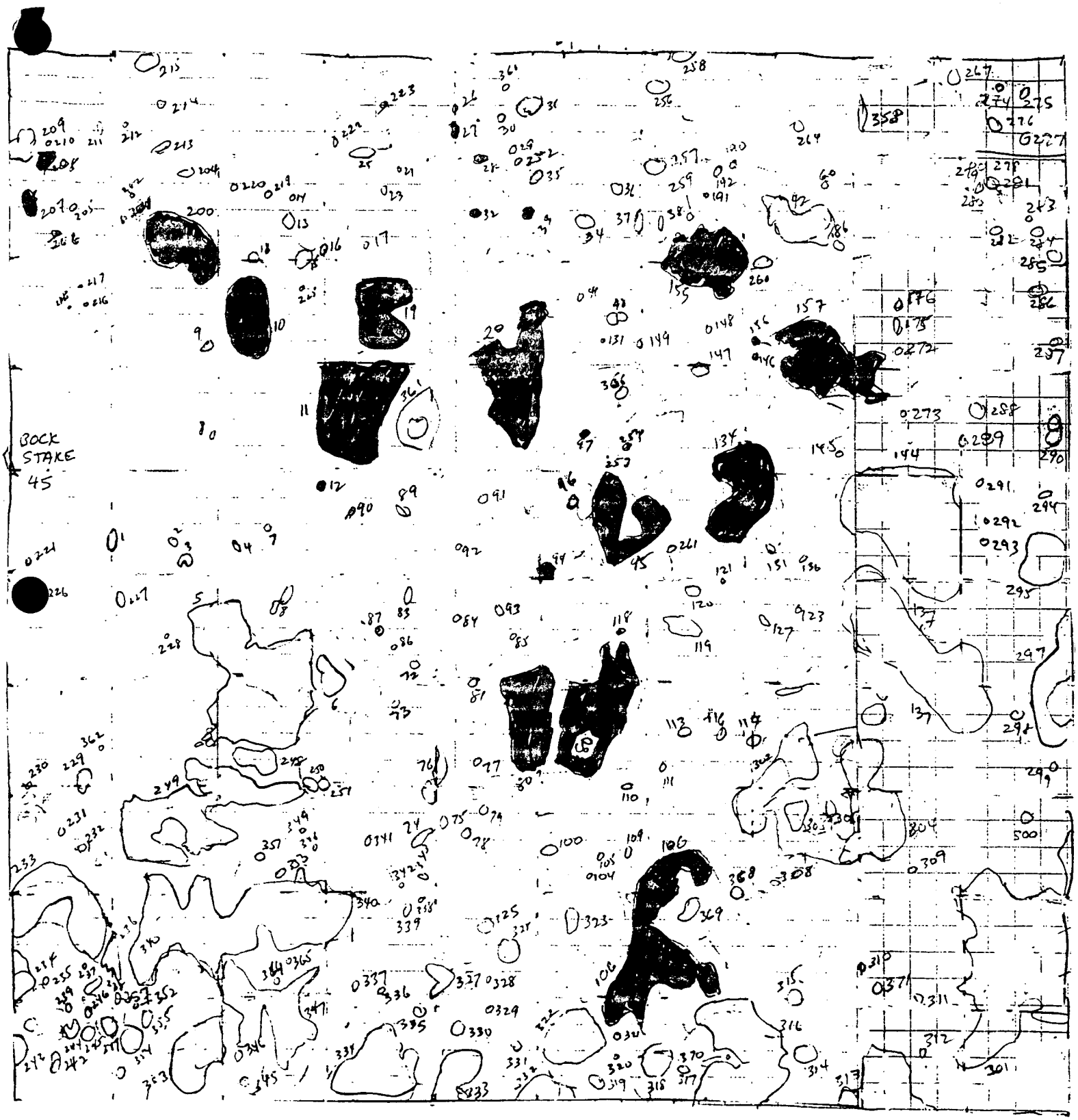

PLOT 36
1m.
N
60 CHROMOSOMES
90 CHROMOSOMES
/// OTHER NUMBER OF CHROMOSOMES (INTERMEDIATE)
NOT TESTED

PLOT 45



N

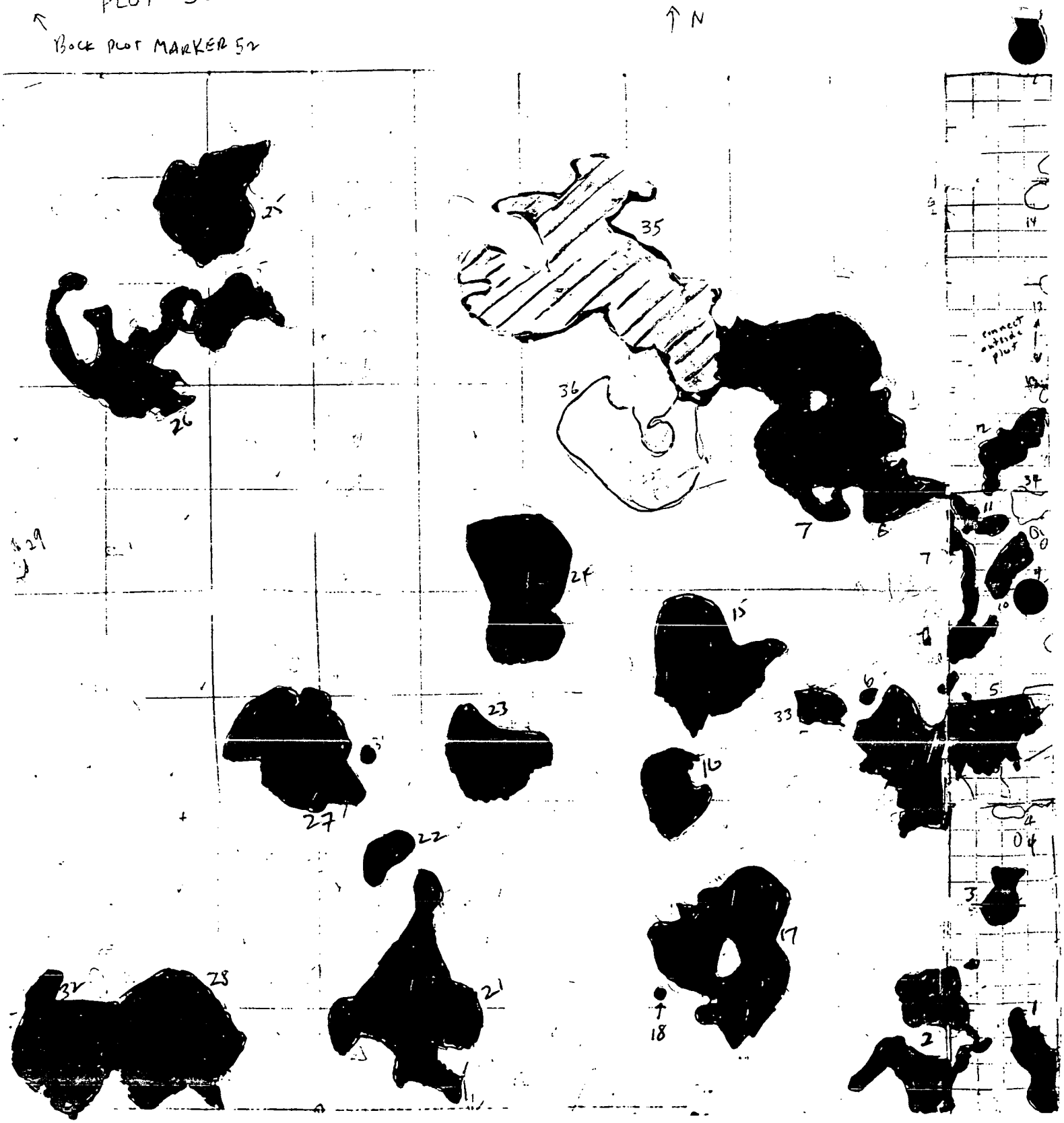
■ 60 CHROMOSOMES
■ 90 CHROMOSOMES
▨ OTHER (INTERMEDIATE) CHROMOSOME NUMBER (=91)
□ NOT TESTED

WORKING MAP INCLUDES ROCKS AND OTHER SPECIES AS LAND MARKS

PLOT 52

↖ BACK PLOT MARKER 52

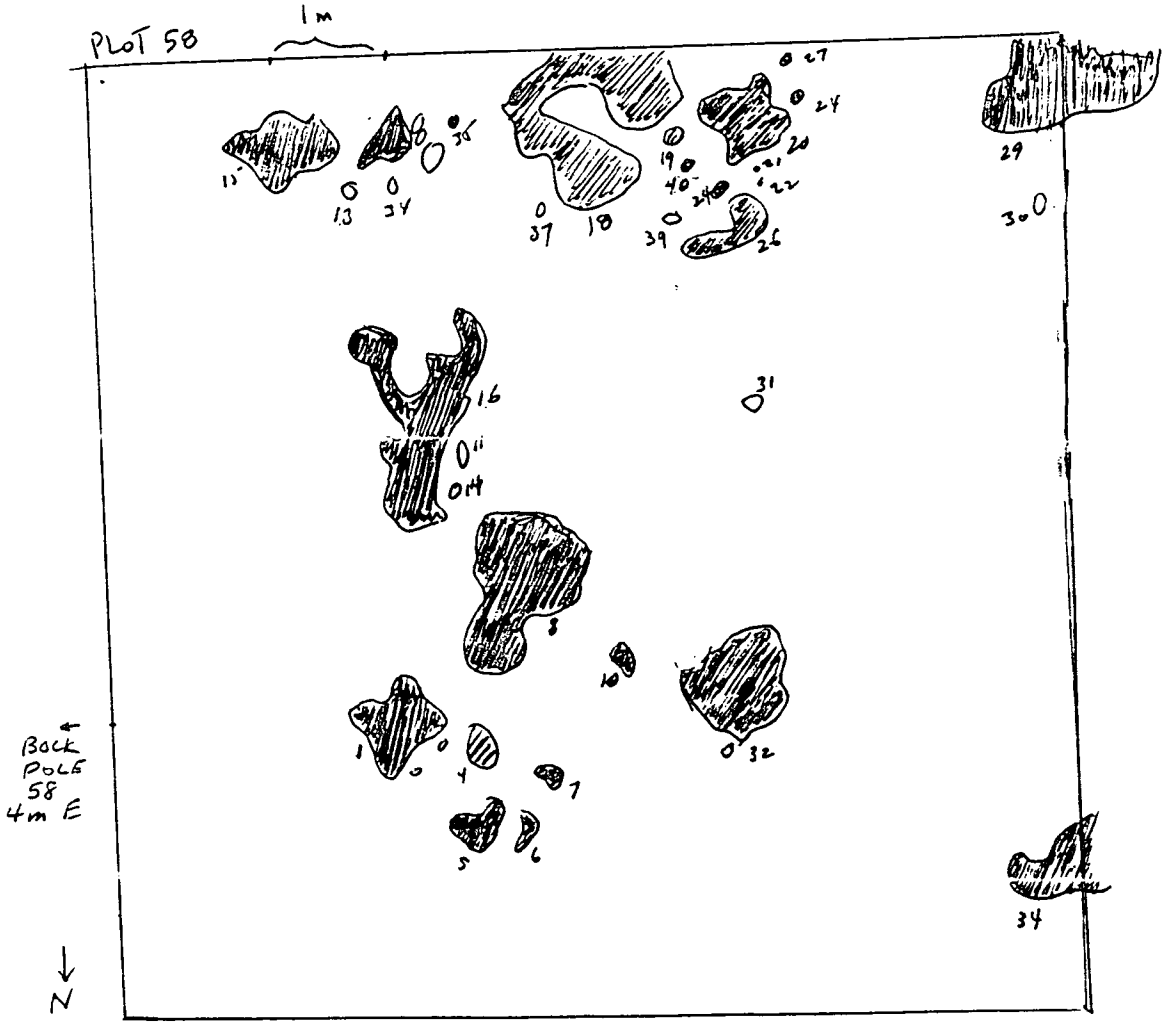
↑ N



WORKING MAP INCLUDES ROCKS AND OTHER SPECIFICS AS LANDMARKS

■ 60 CHROMOSOMES
■ 90 CHROMOSOMES
▨ OTHER (INTERMEDIATE) CHROMOSOME NUMBER (35)
□ NOT TESTED

3 M W, 3 M N of SW corner



20 very low 4.81