Heritability Estimates and Gene Effects for Basal Spikelet Sterility and Other Agronomic Characters in Four Crosses of Winter Wheat (*Triticum aestivum* L. em. Thell.)

by

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INTRODUCTION

The wheat spike is an example of parallel development of morphologically similar structures, namely, the spikelets and florets. The spike consists of an axis upon which are arranged two opposite rows of spikelets. Each spikelet consists of an axis upon which are arranged two rows of florets. The apical and basal spikelets are often sterile, and in each spikelet the third floret (counting from the base) is often sterile and the fourth floret usually sterile. Apart from these differences, the spikelets and florets are indistinguishable at maturity. This similarity emphasizes the interest of the action of the 'sterile base' genotypes which condition a sterility of the basal floret of each spikelet.

Considerable emphasis is placed on yield improvement in wheat (Triticum aestivum L. em Thell.). The effort to improve the wheat plant has involved various plant characters.

Yield component breeding and the modification of the plant architecture offer possibilities to develop more efficient breeding systems for increased grain yield.

Fertile spikelet number per ear in wheat is an important yield component which has been suggested to be under single genetic control. It is the product of the rate and duration of spikelet initiation plus the number of double ridges (spikelet primordia) present at floral initiation.

The present study was conducted to estimate heritability and gene effects for basal spikelets sterility and other agronomic traits in four common winter wheat crosses.

LITERATURE REVIEW

The term "sterility" will be used to denote both phenomena of non-development of grains in the tip spikelets as well as in the base spikelets. Sterile spikelets are those that do not develop seed. If one grain was produced the spikelet was classed as fertile.

In the case of the "tip sterility" the flowers are present in the spikelets but they fail to develop seeds and the spikelets dry up. In the case of the "base sterility" the spikelets are small, rudementary and the flowers also fail to develop seeds. The differences between varieties concerning the degree of sterility of the basal spikelets are known to the breeders.

The inheritance of sterility of spikelets was studied by Jasnowski (16). No correlation for sterility was found between spikelets at the base of the spike and those at the tip, indicating independent inheritance. The data also indicated that sterility of the basal part of the spike was determined by two pairs of cumulative factors. Sterility and fertility of the upper part of the spike apparently involved an independent pair of alleles with fertility dominant. Basal sterility has also been found to be dependent on a single recessive gene (27).

Perrin(22) believes that environmental conditions influence the degree of sterility of the basal part of the ear. Quittet, see Boeuf 1932 (6) expresses the opinion that such conditions have little if any influence on the degree of sterility.

The degree of development of the basal spikelets of the spikes of sensitive varieties (short day sensitivity) like Thatcher depends upon the length of the daylight periods during the early stages of growth - long days result in full development while short days result in rather rudimentary development. Sometimes, as in the case of club wheats, spike shape can reflect variations in day length. Three American winter wheats - Blackhull, Early Blackhull, and Extra Early Blackhull - appear to differ rather strikingly in their sensitivity to photoperiod (23).

A comparative response of alloplasmic and euplasmic wheats to photoperiod and vernalization studied by Ward(30)showed that, increased duration of vernalization (from 6 to 8 weeks) decreased basal spikelets sterility and potential spikelet number per spike. Increase day length (from 17/7 hr to 20/4 hr) reduced potential spikelet number, but increased the basal spikelet sterility. In another photoperiod treatment (14/10 hr and 16/8 hr) there were no significant effects for this treatment concerning basal sterility while increase day length in this treatment, reduced the potential spikelet number. Mean reductions associated with increased day length were also found for flag leaf length, flag leaf width and plant height.

Another study(13)reported the following:

1. The number of sterile spikelets per spike in wheat is directly affected by the rate of seeding or the spacing of the plants. The more space allowed each plant the fewer sterile spikelets on each spike.

2. The awned varieties of wheat as a class had a higher percentage of sterile spikelets than the awnless varieties. Of the 188 varieties examined the smallest number of sterile spikelets was found

on a awnless variety and the largest number on a awned variety.

3. Early seeding seems to increase the percentage of sterile spikelets on each spike. Wheat seeded late had the smallest percentage of sterile spikelets.

4. The application of nitrogen alone as a fertilizer produced the lowest percentage of sterile spikelets. Phosphoric acid singly gave the highest percentage of sterile spikelets, while potash was intermediate as to the percentage of sterile spikelets. Where two elements of fertilizers were combined, phosphoric acid and potash gave the highest percentage of sterile spikelets, with nitrogen and phosphoric acid next and nitrogen and potash last. In every instance the check or untreated plots gave a lower percentage of sterile spikelets than those treated with a complete fertilizer.

5. There was a distinct correlation between the length of spike as expressed by the number of spikelets and the number of sterile spikelets. As the number of spikelets per spike increases (in other words, the length of spike), the number of sterile spikelets becomes greater. That is, varieties with the shorter spikes tend toward a smaller number of sterile spikelets than the varieties with the longer spikes. However, the percentage of sterile spikelets per spike may be greater among the varieties with the shorter spike, as was shown to be the case where spikes of varying lengths within a single variety were examined.

6. There was only a very slight correlation between the percentage of sterile spikelets and the number of tillers to each plant.

7. The yield of grain per plant was correlated to a fair degree with a low percentage of sterile spikelets.

8. The weight of the kernel or quality of grain was correlated to a considerable degree with a low percentage of sterile spikelets.

9. The yield of grain per spike, the length of spike, and the length of culm were strongly correlated with a low percentage of sterile spikelets.

10. There was a slight correlation between the average number of spikelets per spike and a low percentage of sterile spikelets.

Heritability Studies

Heritability is used in both a "broad sense" and a "narrow sense"(19). In the broad sense, heritability considers total genetic variability comprising additive, dominance, and epistasis in relation to the total phenotypic variability; while heritability in the narrow sense considers only the additive portion of the genetic variability.

Several methods have been proposed for estimating the degree of heritability in crop plants of these, the parent - offspring regression method proposed by Lush (19)is widely used in self-pollinating species. This technique involves the regressing the mean value of a characteristic in the progeny upon the value of the same characteristic in the parent. The regression values are converted directly to heritability percentages. In cross pollinated plants, where both parents are measured, the regression on one parent is doubled to obtain the heritability estimate.

Since parent-offspring regressions for characteristics in crop plants are computed by regressing data collected in one year upon data obtained in the previous year, any environmental factor could change the range of phenotypic variation from year to year which may overestimate heritability and values greater than 100% may be obtained. To avoid such situations, Frey and Horner (11) proposed a method called standard unit or correlation method. Standard unit heritabilities are obtained by computing the regressions on data coded in terms of standard deviation units for each character under study. Such a regression is identical to correlation coefficients on the original data. According to the authors, this method eliminates the environmental effects of different years which increase or decrease the range of the progenies relative to that of the parent by establishing a heritability ceiling of 100%. Thus, the standard unit method eliminates the unrealistic heritability values greater than one.

To avoid overestimates, of heritability, regardless of the degree of inbreeding or breeding system, Smith and Kinman (28) proposed an adjusted method in self-pollinated plants. According to them, the regression coefficient should be divided by twice the probability that a random gene at a specific locus in one parent (x) is identical by descent to a random gene at the same locus of the other parent (y), then H^2 (heritability) = $b/2r_{xy}$. The adjusted heritabilities are based on the genetic variance of a random breeding population.

Heritabilities are also estimated by variance component method in which the variance components are obtained by equating the mean squares to their expectations. Robinson et al. (25) used this method in corn.

A method of estimating heritability from the variances of three types of segregating populations the F_2 and the summed backcrosses to each parent was reported by Warner (31). According to him, this method has the advantage of not requiring an estimate of environmental or of total genetic variance but uses only total within-population variance. Thus, this method is an approach to estimate heritability in the narrow sense. However, it is pointed out that nonheritable variances of the F_2 and backcrosses should be approximately similar in magnitude.

Heritability has value primarily as a method of quantifying the concept of whether progress from selection for a plant character is relatively easy or difficult in a breeding program (14). A high heritability in the narrow sense indicates that reliance may be placed on mass selection and as heritability becomes lower emphasis should be on pedigree method of breeding with progeny tests and selection. Heritability in the narrow sense may be used to estimate expected genetic gain due to selection. Formulas for computing expected response to selection for various breeding schemes are given by Allard (2), Comstock and Robinson (9), Falconer (10), and Sprague (29).

Heritability estimates are dependent on the method by which they are estimated, the genetic populations from which the estimates are obtained, the unit of measurement, and the environmental conditions encountered during the test. Warner (31) grouped methods of estimating heritability into three principal classes as those based on

1. Parent-offspring regressions.
2. Variance components from an analysis of variance.
3. Approximation of nonheritable variance from genetically uniform populations to estimate total genetic variance.

Heritability estimates reported by several workers tended to indicate that certain morphological traits which influence grain yield in wheat are more heritable than yield itself. Reddi et al.(24) found relatively high heritability estimates for culm length and kernel weight in two wheat crosses. Low heritability values on the other hand were reported for grain yield in a study of hard red winter wheat by Johnson et al. (17) Heritability estimates were very high for heading date, moderately high for kernel weight and plant height, moderate for tiller number, and low for spikelets per spike, kernels per spike, kernels per spikelet and grain yield in a study of winter wheat cross by Ketata et al.(18).

Gene Effects

Estimates of gene effects have a direct bearing on the method of hybridization and selection to be adopted in breeding programs. The magnitude of additive effects is particularly useful to the wheat breeder involved in developing pure-line varieties; whereas, information concerning dominance and epistatic gene effects can be valuable in the development of hybrid wheat. A model for partitioning the genotypic value into additive, dominant, and epistatic gene effects was provided by Anderson and Kempthorne(4). This method employs the means of populations obtained from crossing two homozygous lines followed by selfing. Six parameters, K_2, E, F, G, L. and M, were derived where K_2 represented mean effects and E and F represent non-epistatic effects. Some of these parameters are difficult to interpret because of pooled gene effects in the parameter. Cockerham (8) and Mather(21) proposed models for partitioning genetic variances into the above compounds. All these models, however, are primarily based on factorial statistical experiements.

Hayman (15) described parameters which estimates the additive, dominant, additive X additive, additive X dominant, and dominant X dominant with less difficulty in interpretation. However, where significant epistasis is present, additive and dominant gene effects are difficult to separate and the relative contributions of the types of gene action to various genetic phenomenon cannot be interpreted by the partitioning method (15).

Using the means of six population, $\overline{P}_1$, $\overline{P}_2$, $\overline{F}_1$, $\overline{F}_2$, $\overline{B}_1$ ($\overline{P}_1$ X $\overline{F}_1$), and $\overline{B}_2$ ($\overline{P}_2$ X $\overline{F}_1$), Gamble (12) outlined a procedure to estimate 6 parameters, namely mean effects, additive and dominant gene effects, and the three types of digenic epistatic effects.

Estimates of gene effects calculated by Hayman's method (15) were reported in pearl millet (1, 20, 26). Results obtained by Singh et al. (26) showed that additive gene effects were highly significant for all the characters except for number of branches. Except days to flower, all the characters were associated with highly significant dominant gene effects. The additive X dominant type of digenic epistatic effects were less important than the other two types of non-allelic interactions. Duplicate epistasis was exhibited by plant height, number of internodes, stem thickness, number of tillers, number of spike-bearing tillers, number of spike-bearing branches, leaf breadth, days to flower, and 250 grain weight and complimentary epistasis was observed for number of branches, leaf length, peduncle length, peduncle thickness, spike length, and spike thickness.

Working with durum wheat, Amaya et al. (3) found that dominance gene effects predominated in the inheritance of grain yield, whereas, mostly additive effects controlled plant height and heading date. Bhatt (5)

reported that gene action involved in the inheritance of heading date, plant height, and kernel weight of two spring wheat crosses was primarily of the additive type. Chapman and McNeal(7) found that epistasis was involved in the expression of tiller number, grain yield, and plant height, but there were no significant epistatic effects for spikelets/spike and kernel weight in a spring wheat cross.

MATERIALS AND METHODS

The four wheat lines used in this study were obtained from DeKalb Seed Company (see Table 1). Contrasting characteristics of these parents were number of sterile spikelets at the base of the spike, plant height, grain weight, kernel weight and seed set.

Two crosses, including 6 populations and two crosses including 4 populations, were studied as follows:

Cross 1: P_1 (R108) as male, P_2 (AI24) as female, their F_1, F_2, B_1 (F_1 X P_1), and B_2 (F_1 X P_2) derivatives.

Cross 2: P_1 (R100) as male, P_2 (AI24) as female, their F_1, F_2, B_1 (F_1 X P_1), and B_2 (F_1 X P_2) derivatives.

Cross 3: P_1 (R108) as male, P_2 (AB123) as female, their F_1, and F_2 derivatives.

Cross 4: P_1 (R100) as male, P_2 (AB123) as female, their F_1, and F_2 derivatives.

In 1980, the materials (parents, F_1 hybrids and 'Newton' as standard) were seeded on the Ashland Agronomy farm, Manhattan, Kansas, in a randomized complete block design with three blocks, 9 genotypes (4 parents, 4 F_1 hybrids, 1 Newton) 3 observations for each genotype/block {total 27 plots/block} and three rows were spaced 7 inches apart and 36 inches long. One hundred seeds were seeded per plot.

Table 1. General description of parental wheat genotypes used in the study

Genotype	General description
AI 24 (Bezastia), cms* (A-line) I 24 (Bezastia selection), (B-line)	Low basal sterility (mean = 1.32), intermediate height, awnless, glaborous, large seed.
AB 123, cms (A-line) B-123, (B-line)	Intermediate basal sterility (mean = 2.95), semi-dwarf, awned, glaborous.
R108, (R-line)	High basal sterility (mean = 3.25), tall, awned, glaborous.
R100, (R-line)	Intermediate basal sterility (mean = 2.17), tall, awned, pubescent.

*Cytoplasmic male sterile.

All the crosses between parental lines, selfing of F_1 hybrids and backcrosses of F_1 hybrids of crosses 1 and 2 (the most contrasting ones) were made in May 1980.

The 6 populations of crosses 1 and 2 and the 4 populations of crosses 3 and 4 were seeded October 1980 at Ashland Agronomy farm. The crop was grown on dry land. The experimental design was randomized complete block design with 4 replications, 18 plots/replications. Plots consisted of 3 rows 80 inches long, 12 inches between rows and 2 inches between seed in each row. There were 120 seeds/plot (40/row) for each entry. The borders between plots were Newton. For parential lines and F_1's, 10 random plants from each plot were chosen while 20 random plants were chosen for F_2's and backcrosses to record observations for all of these populations. All the characters were measured on an individual spike basis concerning the 1980 study (parental lines and F_1's) and on individual plant basis in the 1981 study (parental lines, F_1, F_2, BC_1, BC_2).

The following measurements were recorded for each character measured:

1. Plant height: distance (cm) between the base of the culm and the tip of the spike on the tallest tiller, awns excluded if any.

2. Collar height: distance (cm) between the base of the culm and the base of leaf blade of the flag leaf on the talllest tiller.

3. Culm height: distance (cm) between the base of the culm and the base of spike (spike excluded) on the tallest tiller.

4. Peduncle length: distance (cm) between the base of the spike and the top node.

5. Spike length: length (cm) of the spike on the tallest tiller.

6. Flag leaf width: width (cm) of the flag leaf on the tallest tiller.

7. Flag leaf length: length (cm) of the flag leaf on the tallest tiller.

8. Spikelet number: number of spikelets per spike on the tallest tiller.

9. Base sterile spikelet number: number of sterile spikelet (do not develop seeds at all) at the base of the spike on the tallest tiller.

10. Tip sterile spikelet: presence of sterility at the tip of the spike on the tallest tiller.

11. Seed set number: number of seed on the spike of the tallest tiller.

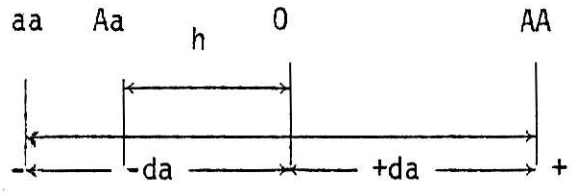
12. Grain weight: weight (gm) of seeds per spike on the tallest tiller.

13. Kernel weight: Mean weight (gm) of each seed per spike on the tallest tiller (multiplying by 1000 will give the weight of 1000 seeds).

Statistical Treatment of the Data

From the 1980 data which represented parental lines and F_1 hybrids only, analyses of variance for all characters were calculated. Mean performance of the parents and F_1's for 14 characters in four crosses were calculated. Gene effects which referred to as h-value (the deviation of heterozygote F_1 from the mid-parent) as calculated by Mather (21) for the 14 characters in four crosses were estimated. From these analyses, heritability in broad sense using variance components from analysis of variance method was calculated.

$$\text{h-value} = \frac{F_1 - \text{mid-parent}}{1/2\ (P_1 - P_2)}$$



If

h = o : no dominance, (F_1 = mid-parent)

h > da : over dominance

h < da : under dominance

h = da : full dominance

h > o, and < da : partial dominance

From the 1981 data which represented parental lines, F_1, F_2, BC_1 and BC_2, analyses of variance for all characters were calculated.

Warner's (31) method of estimating heritability from the variances of three types of segregating populations, the F_2 and the summed backcrosses to each parent, were employed to obtain heritability values in narrow sense for all the characters. The F_2 phenotypic variance was expressed as follows:

V_{F_2} = 1/2 D + 1/4 H + E where D, H, and E represent additive, dominant, and environmental variances respectively.

The sum of the variances of backcross to parent 1 and 2 may be expressed as follows:

$$(V_{B_1} + V_{B_2}) = 1/2\ D + 1/2\ H + 2E$$

The difference between twice the variance of the F_2 generation and the sum of the two first backcross generations was attributed to additive gene effects. Thus the additive genetic variance in F_2 could be estimated from the expected mean square of F_2 and backcrosses, i.e.,

$$1/2\ D = 2\ V_{F_2} - (V_{B_1} + V_{B_2})$$

Warner's method of estimating heritability would then be expressed as follows:

$$h^2 = \frac{\{2V_{F_2} - (V_{B_1} + V_{B_2})\}}{V_{F_2}} \times 100$$

Heritability estimates in broad sense would then be expressed as follows:

$$h^2 = \frac{V_{F_2} - V_{F_1}}{V_{F_2}} \times 100$$

Information on the nature of gene action involved for all the characters was obtained by the method developed by Anderson and Kempthorne (4), Hayman(15)and modified by Gamble(12). This procedure would be of specific use in situations where the individual genotypes are not identifiable but where average genetic expectations are known. Thus, with the means of only 6 populations, $\overline{P}_1$, $\overline{P}_2$, $\overline{F}_1$, $\overline{F}_2$, $\overline{B}_1$, $\overline{B}_2$, 6 parameters were estimated as follows:

$$m = \overline{F}_2$$

$$a = \overline{B}_1 - \overline{B}_2$$

$$d = -1/2\ \overline{P}_1 - 1/2\ \overline{P}_2 + \overline{F}_1 - 4\overline{F}_2 + 2\overline{B}_1 + 2\overline{B}_2$$

$$aa = - 4\overline{F}_2 + 2\overline{B}_1 + 2\overline{B}_2$$

$$ad = - 1/2\ \overline{P}_1 + 1/2\ \overline{P}_2 + \overline{B}_1 - \overline{B}_2$$

$$dd = \overline{P}_1 + \overline{P}_2 + 2\overline{F}_1 + 4\overline{F}_2 - 4\overline{B}_1 - 4\overline{B}_2$$

Where m = the F_2 mean

a = additive gene effects

d = dominance gene effects

aa = additive X additive epistatic gene effects

ad = additive X dominant epistatic gene effects

dd = dominant X dominant epistatic gene effects

Significant of these genetic effects was evaluated by the corresponding standard error obtained from the analyses of variance of the population means.

RESULTS AND DISCUSSION

The mean performance of initial data (parental lines and F_1 hybrids) tested during 1980 are given in Table 2. R108 was the highest and AB123 was the lowest for the following characters: plant height, collar height, culm height, peduncle length, number of spikelets/spike, number of seeds/spike. AI24 was the highest and R108 was the lowest for flag leaf width, kernel weight, and tip sterility characters. AI24 was the highest and AB123 was the lowest for flag leaf length, spike length, and grain weight characters. R108 was the latest and R100 was the earliest for flowering date. R108 was the highest and AI24 was the lowest for basal spikelet sterility character.

The F_1 deviated from the mid-parental value for all characters except flag leaf width and kernel weight in crosses 1 and 2 and showed a sizeable amount of non-additive gene action (Table 2). Flag leaf width and kernel weight in crosses 1 and 2 showed no dominance effects (Table 2).

The means and variances for the six populations in crosses 1, 2 and for the four populations in crosses 3, 4 are presented in Table 3. R108 had the highest mean collar height, culm length, peduncle length, number of spikelet/spike, basal sterility, tip sterility, number of seeds/spike, and plant height characters, while AI24 had the highest mean flag leaf width, and grain weight characters. R100 had the highest values for flag leaf lenght, spike length, and kernel weight characters. AB123 had the lowest mean for most of the characters.

Table 2. Mean performance, h-value for parents and F_1's for 14 characters in four wheat crosses.

Cross	P_1	P_2	F_1	mid-parent	h-value
			Flag leaf width (cm)		
1	1.08	1.43	1.25	1.25	0
2	1.08	1.43	1.25	1.25	0
3	1.08	1.18	1.16	1.13	0.6
4	1.08	1.18	1.16	1.13	0.6
			Flag leaf length (cm)		
1	16.75	20.03	18.11	18.39	-0.17
2	18.12	20.03	20.33	19.07	1.30
3	16.75	15.41	17.01	16.08	1.39
4	18.12	15.41	17.93	16.76	0.85
			Collar height (cm)		
1	77.94	69.98	81.16	73.96	1.81
2	72.62	69.98	78.51	71.30	5.46
3	77.94	57.80	75.07	67.87	0.62
4	72.62	57.80	70.26	65.21	0.68
			Plant height (cm)		
1	99.55	83.26	104.45	91.40	1.6
2	95.51	83.26	102.78	89.38	2.18
3	99.55	70.60	98.19	85.07	0.91
4	95.51	70.60	91.43	83.05	0.67
			Flowering date (May)		
1	25.16	24.69	22.79	24.92	-8.88
2	22.32	24.69	22.04	23.50	-1.24
3	25.16	23.10	22.83	24.13	-1.26
4	22.32	23.10	24.22	22.71	3.87
			Spike length (cm)		
1	8.28	8.75	8.55	8.51	0.13
2	8.22	8.75	8.92	8.48	1.59
3	8.28	7.48	8.04	7.88	0.40
4	8.22	7.48	8.32	7.85	1.27

Table 2. (continued)

Cross	P_1	P_2	F_1	mid-parent	h-value
			Culm length (cm)		
1	91.27	74.51	95.90	82.89	1.65
2	87.29	74.51	93.87	80.90	2.03
3	91.27	63.12	90.14	77.19	0.92
4	87.29	63.12	83.11	75.20	0.65
			Peduncle length (cm)		
1	54.28	43.27	56.72	48.77	1.44
2	43.77	43.27	53.80	43.52	41.12
3	54.28	35.79	53.45	45.03	0.91
4	43.77	35.79	44.24	39.78	1.12
			No. of spikelets/spike		
1	19.23	18.54	19.20	18.88	0.89
2	16.66	18.54	17.67	17.60	0.07
3	19.23	16.49	17.89	17.86	0.02
4	16.66	16.49	16.96	16.57	4.33
			No. of Basal spikelet sterility/spike		
1	3.64	1.56	2.31	2.60	-0.28
2	2.28	1.56	1.48	1.92	-1.24
3	3.64	2.80	3.14	3.22	-0.19
4	2.28	2.80	2.37	2.54	-0.66
			No. of tip spikelet sterility/spike		
1	0.06	0.16	0.01	0.11	-1.92
2	0.11	0.16	0.02	0.13	-4.52
3	0.06	0.08	0.11	0.07	4.00
4	0.11	0.08	0.18	0.09	5.4
			No. of seeds/spike		
1	34.79	26.01	36.91	30.40	1.48
2	27.35	26.01	33.33	26.68	9.93
3	34.79	18.54	31.19	26.66	0.56
4	27.35	18.54	26.29	22.94	0.76

Table 2. (continued)

Cross	P_1	P_2	F_1	mid-parent	h-value
			Grain Weight (g)		
1	1.04	1.07	1.30	1.05	12.97
2	0.99	1.07	1.27	1.03	5.85
3	1.04	0.68	1.13	0.86	1.50
4	0.99	0.68	1.04	0.83	1.32
			Kernel weight (g)		
1	0.029	0.041	0.035	0.035	0
2	0.035	0.041	0.038	0.038	0
3	0.029	0.036	0.036	0.032	1
4	0.035	0.036	0.040	0.035	8