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Effects of Different Markers Frequency for Marker Assisted Introgression Efficiency

Jun Yan Bai,[1,]* Xiao Ping Jia,[2] You Bing Yang,[1] You Zhi Pang[1] and Yan Xia Qi[1]

[1]College of Animal Science and Technology, Henan University of Science and Technology, Henan, Luoyang 471003, China

[2]College of Agriculture, Henan University of Science and Technology, Henan, Luoyang 471003, China

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Authors' Contribution

JYB conceived and designed the study, collected samples, analyzed the data and wrote the article. YZP helped in sampling. YBY and YXQ helped in analysis of data. XPJ helped in writing of article.

Key words

Marker-assisted introgression, QTL, Flanking markers selection, MBLUP selection

ABSTRACT

The objective of this study was to analyze the effect of non-unique marker on marker-assisted introgression efficiency to compare the effects of the flanking markers selection and MBLUP selection on marker-assisted introgression efficiency, and to provide the reference for implementing marker-assisted introgression in practice. The results showed that as for flanking markers selection, introgression QTL frequency was increased with the marker allele frequencies. And as for MBLUP selection, introgression QTL frequency did not change with the marker allele frequencies. Even when the marker allele frequencies in the basic group were very low, the very high introgression QTL frequency was still obtained. When the allele marker frequency was 0.5/0.5, after athwart cross for 5 generations, introgression QTL frequencies still reached 0.9629. Therefore, when the marker alleles are distributed in two basic groups with a certain frequency, MBLUP method is suggested for foreground selection.

INTRODUCTION

Since 1980s, with the rapid development of molecular biological technology, especially the completion of human genome DNA sequencing, the research progress of animal genome project was greatly promoted. With the constant deepening of the research on the animal functional genomics, major gene resistance or quantitative traits loci affecting important economic traits in livestock and poultry were located using DNA molecular markers by candidate gene and genome scanning methods (Dekkers, 2004). More and more functional genes having important economical significance were explored (Bai *et al*., 2016), which provided many opportunities for animal breeding. These genes or linked marker information would further improve the efficiency of animal breeding. More importantly, it could solve some problems that could not be solved with traditional breeding methods. One of the promising opportunities was to cultivate the more ideal varieties (lines) through introgression (Dekkers and Hospital, 2002). Based on the high density genetic map, QTL detection and its positioning basis, marker-assisted introgression could be performed (Frisch and Melchinger, 2001a,b; Frisch *et al*., 1999; Koudandé *et al*., 2000; Chaiwong *et al*., 2002). Genetic markers had the following two uses in marker-assisted introgression (Visscher *et al*., 1996; Visscher and Haley, 1999) one was to identify the existence of the introgression using marker information. In each generation, to track the existence of the target genes like a diagnostic tool could accurately select introgression carriers. The other was to select or exclude a certain specific background genome using genetic markers, which could accelerate the recovery speed of receptor genetic background, while effectively eliminating the adverse genes linked with introgression gene. Two kinds of strategies including flanking markers selection and MBLUP selection were adopted aiming at non-specific marker in the paper, so as to provide the reference for implementing marker-assisted introgression in practice.

MATERIALS AND METHODS

Experimental design

It was supposed that there was no relationship between all individuals of donor group and receptor group in basic group. The sib-mating should be avoided in all generations. The offspring sex ratio was determined according to 1:1 probability. All generations were not overlapped. It was supposed that the entire genome was distributed in 10 chromosomes. All markers were evenly distributed in each chromosome. There were 2 alleles in each marker locus. The original marker allele frequencies (donor/receptor) was 0.95/0.05, 0.90/0.10, 0.80/0.20, 0.70/0.30, 0.60/ 0.40 and 0.50/0.50. It was supposed that introgression QTL was taken as QTL. The background QTL was taken as QTL_1 and QTL_2.

* Corresponding author: junyanbai@163.com
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Phenotypic value of traits

(1) Phenotypic value of traits *y* in basic group:

$$y_i = q_i + u_i + e_i$$

Among them, y_i was phenotypic individual *i*, *q* was QTL genotypic value of individual *i*, u_i was multi gene effect value of individual value of *i*. As for two parental populations, u_i was randomly generated by normal distribution *N*0, σ_u^2 e_i was random environmental deviation of individual *i*. In all generations, e_i was randomly generated by the normal distribution $N(0, \sigma_e^2)$.

(2) The method to generate individual phenotypic value in non-basic group was similar with that of basic group. The calculation of multi phenotypic effect value was different:

$$u_i = 0.5u_s + 0.5u_d + m_i .$$

Among them, u_i was multi gene effect value of individual *I*, u_s and u_d were individual paternal and maternal *i* multi gene effect value, m_i was Mendelian sampling deviation of individual *I*, obeying the normal distribution $N(0, (\sigma_u^2/2)(1-(F_s+F_d)/2))$,. F_s and F_d were paternal and maternal inbreeding coefficient.

Selection method

(1) Flanking markers selection: It was supposed that introgression QTL itself was unknown. Meanwhile flanking markers which were the nearest neighbors with introgression QTL were used for indirect selection. Two individuals which the markers were heterozygous were selected and called flanking markers selection.

(2) Marker-assisted BLUP selection. The breeding value of individual foreground traits was estimated by the animal model MBLUP. The breeding stock was selected according to the breeding value. According to mixed model proposed by Femando *et al.* (1989), if it was supposed that the random QTL effect and random polygenic effect were the genetic basis of traits, individual phenotypic value could be described with the following linear models in the form of matrix:

$$y = Zu + Wv + e$$

Among them, *y* was traits observation value vector, u was random residual polygenic effect value vector, its mean value was 0. The variance covariance matrix was $A\sigma_u^2$. Among them, *A* was molecular genetic correlation matrix, v was random QTL allelic effect vector, its mean value was 0. The variance covariance matrix was $G\sigma_v^2$, *G* was QLT gametes correlation matrix, e was the residual vector, its mean value was 0. The variance covariance matrix was $I\sigma_e^2$, Among them, I was unit vector, *W* and *Z* were matrix structure of *v* and *u* respectively.

RESULTS AND DISCUSSION

Favorable allele frequency of introgression QTL

The favorable allele frequency of introgression QTL was shown in Table I, you can see flanking markers selection, introgression QTL frequency showed a downward trend with the increase of backcross generation. After backcross for 5 generations, the original marker allele frequencies were 0.5/0.5, 0.6/0.4, 0.7/0.3, 0.8/0.2 and 0.9/0.1. The introgression QTL frequencies were 0.0192, 0.0253, 0.1035, 0.1550, 0.2122 and 0.2289 under 0.95/0.05. By athwart cross, introgression QTL frequency showed an upward trend with the increase of athwart cross generation. Especially athwart cross for 1 to 2 generation, this upward trend was more rapid. After athwart cross for 5 generations, the introgression QTL frequencies of the six original marker allele frequencies reached maximum 0.0221, 0.0490, 0.2821, 0.5739, 0.7994 and 0.8966. The introgression QTL frequencies of the later three were much larger than those of the previous three. The introgression QTL frequency showed an upward trend with the increase of original marker allele frequency in donor. Thus, to increase original marker allele frequency in donor could obtain the higher introgression QTL frequency. And when the original marker allele frequency in donor was very low, the introgression QTL almost lost entirely. Because the recognition of introgression QTL was selected by closely linked flanking markers, when the original marker allele frequency in donor was very low, the probability of error would increase, resulting in the loss of introgression QTL.

When MBLUP was selected, the introgression QTL frequencies had no difference between original marker allele frequencies. After athwart cross for 5 generations, the original marker allele frequencies were 0.5/0.5, 0.6/0.4, 0.7/0.3, 0.8/0.2 and 0.9/0.1. The introgression QTL frequencies were increased to 0.9629, 0.9966, 0.9931, 0.9950, 0.9985 and 0.9981 under 0.95/0.05. The introgression QTL frequency of the original marker allele frequency 0.5/0.5 was relatively low, other original marker allele frequencies were relatively close. Compared with flanking markers foreground selection, the effect of MBLUP selection was better than that of flanking markers selection. Especially when the original marker allele frequency 0.5/0.5 was relatively low, the introgression QTL frequency obtained by MBLUP selection still reached 0.9629 after athwart crossing for 5 generations, while the flanking markers selection result was only 0.0221. Thus, when the original marker allele

was distributed in the donor and receptor with a certain frequency, the foreground selection using MBLUP selection had more advantages.

Genetic progress of foreground traits

The trend of foreground traits genetic advances between different original marker allele frequencies was shown in Table II. As shown in Table II, as for flanking markers selection, genetic advance of foreground traits showed upward trend with the increase of original marker allele frequency in donor. During backcross stage, the genetic advance of foreground traits showed downward trend with the increase of backcross generations. After backcross for 5 generations, the original marker allele frequencies were 0.5/0.5, 0.6/0.4, 0.7/0.3, 0.8/0.2 and 0.9/0.1. The average breeding values of foreground traits were -4.4593, -4.5629, -3.5936, -3.1073, -2.4034 and -2.390 7 under 0.95/0.05. By athwart cross stage, genetic advance of foreground traits showed an upward trend with the increase of athwart cross generation. After athwart cross for 5 generations, the original marker allele frequencies were 0.5/0.5, 0.6/0.4, 0.7/0.3, 0.8/0.2 and 0.9/0.1. The average breeding value of foreground traits were increased to -4.4627, -4.0563, -1.9749, 0.6810, 2.4754 and 3.3358 under 0.95/0.05. The foreground traits genetic advances with the change of original marker allele frequency was basically consistent with introgression QTL frequency, the reason might be that QTL effect value was too large, its effect on phenotypic value was far larger than that of polygenic effects.

When MBLUP was selected, genetic advances of foreground traits showed no difference between different original marker frequencies. In athwart cross stage, genetic advance showed a rapid upward trend with the increase of generation. After athwart cross for 5 generations, the average foreground traits breeding values were increased by 12.4150, 12.2750, 12.3683, 12.3569, 12.7017 and 12.4029 respectively under six kinds of original marker allele frequencies. Compared with flanking markers foreground selection, MBLUP selection could achieve the better results. Especially when the original marker allele frequency was low, the foreground traits genetic advances obtained was close under 0.5/0.5 and 0.95/0.05 for MBLUP selection. But the flanking markers selection almost did not obtain the genetic advance when the original mark allele frequency was relatively low.

Background QTL frequency

The trend of background QTL frequencies was shown in Table III. between different original marker allele frequencies. Table III showed the changes of background QTL frequencies were consistent under the two strategies. The background QTL frequency showed an upward trend with the increase of original marker allele frequency in donor and showed an upward trend with the generation. As for flanking markers selection, QTL frequencies showed less difference between different original marker allele frequencies with athwart cross generation. After athwart cross for 5 generations, the first background QTL frequencies of the six original mark allelic frequencies were increased by 0.9524, 0.9794, 0.9929, 0.9962, 1.0000 and 1.0000.

Background traits genetic progress

The trend of background traits genetic progress between original marker allele frequencies was shown in Table IV. As for flanking markers selection, the original marker allele frequencies were 0.5/0.5, 0.6/0.4, 0.7/0.3, 0.8/0.2 and 0.9/0.1 after athwart cross for 5 generations. The average breeding values of first background traits were increased to 13.6520, 13.9095, 14.1916, 14.8622, 16.4019 and 19.2994 under 0.95/0.05. The former four results were very close. And the latter two results were much higher than those of the former four. The background traits genetic progress showed an upward trend with the increase of original marker allele frequency in donor, and also showed an upward trend with the increase of generation. As for MBLUP selection, background traits genetic progress showed an upward trend with the increase of original marker allele frequency in donor. However overall, background traits genetic progress of MBLUP selection was slightly lower than that of flanking markers selection.

In many marker-assisted introgression studies, it was supposed that marker alleles were fixed in donor and receptor in basic group respectively (Bai, 2015; Bai *et al*., 2006; Groen and Smith, 1995; Hospital and Charcosset, 1997). But marker alleles were not fixed in two basic groups respectively in practice. The marker alleles were distributed in two basic groups with a certain frequency. The incomplete information would be provided if the marker information was used for indirect introgression QTL selection. van Heelsum *et al*. (1997a, b) simulantly studied the foreground selection of introgression by two kinds of methods when marker alleles were distributed in donors and receptor in basic group with a certain frequency. One was the existence of marker alleles closely linked with target gene, the other was the probability of introgression target allele. The results showed that to increase original marker allele frequency in donor group would increase the efficiency of marker-assisted introgression. But flanking markers selection and MBLUP selection closely linked with introgression QTL were used in this paper, the effect of different original marker allele frequencies on marker-assisted introgression

Table I.- **Introgressed QTL frequencies with respect to different original marker allele frequencies.**

Generation	Flanking markers selection						MBLUP selection					
	0.5/0.05	0.6/0.4	0.7/0.3	0.8/0.2	0.9/0.1	0.95/0.05	0.5/0.05	0.6/0.4	0.7/0.3	0.8/0.2	0.9/0.1	0.95/0.05
1	0.2491	0.2491	0.2486	0.2491	0.2475	0.2475	0.2491	0.2491	0.2491	0.2491	0.2491	0.2491
2	0.1328	0.1319	0.1768	0.2197	0.2331	0.2434	0.2046	0.2179	0.2132	0.2137	0.2216	0.2174
3	0.0652	0.0852	0.1388	0.1902	0.2228	0.2373	0.2083	0.2096	0.2159	0.2094	0.2119	0.2157
4	0.0372	0.0567	0.1222	0.1722	0.2224	0.2331	0.2109	0.2093	0.2088	0.2023	0.2065	0.2195
5	0.0192	0.0253	0.1035	0.1550	0.2122	0.2289	0.2061	0.2122	0.2055	0.2054	0.2180	0.2053
6	0.0243	0.0298	0.1628	0.2846	0.4118	0.4519	0.3524	0.3580	0.3621	0.3607	0.3697	0.3605
7	0.0207	0.0446	0.2687	0.5066	0.7077	0.7602	0.6412	0.6627	0.6644	0.6496	0.6801	0.6714
8	0.0159	0.0480	0.2901	0.5358	0.7633	0.8322	0.8708	0.9045	0.9050	0.8922	0.9160	0.9065
9	0.0203	0.0533	0.2949	0.5684	0.7994	0.8708	0.9475	0.9804	0.9788	0.9710	0.9866	0.9831
10	0.0221	0.0490	0.2821	0.5739	0.7994	0.8966	0.9629	0.9966	0.9931	0.9950	0.9985	0.9981

Table II.- **Genetic responses for foreground trait with respect to different original marker allele frequencies.**

Generation	Flanking markers selection						MBLUP selection					
	0.5/0.05	0.6/0.4	0.7/0.3	0.8/0.2	0.9/0.1	0.95/0.05	0.5/0.05	0.6/0.4	0.7/0.3	0.8/0.2	0.9/0.1	0.95/0.05
1	-2.2378	-2.1156	-2.2428	-2.1078	-2.2124	-2.1909	-0.1127	-0.0813	-0.0504	-0.1047	-0.1235	-0.1119
2	-3.1161	-3.2443	-2.8335	-2.2614	-2.3797	-2.2498	0.2002	0.1541	0.1568	0.2142	0.2159	0.1027
3	-3.7479	-3.8380	-3.2179	-2.6804	-2.3732	-2.2239	0.4034	0.4801	0.4169	0.3294	0.4664	0.4108
4	-4.0823	-4.1198	-3.4089	-2.8333	-2.3897	-2.2798	0.6389	0.6052	0.6159	0.4526	0.6356	0.6557
5	-4.4593	-4.5629	-3.5936	-3.1073	-2.4034	-2.3907	0.6383	0.5956	0.5367	0.5573	0.7977	0.5060
6	-4.4493	-4.4909	-3.1975	-1.9504	-0.7676	-0.5005	4.3214	4.2024	4.1816	4.1973	4.4527	4.1598
7	-4.4719	-4.3693	-2.1193	-0.0332	1.7685	2.2462	8.5637	8.5619	8.6216	8.5282	8.8967	8.5883
8	-4.3276	-4.0840	-1.8190	0.3207	2.1734	3.0636	12.4150	12.2750	12.3683	12.3569	12.7017	12.4029
9	-4.5026	-4.0903	-1.8108	0.6349	2.4091	3.2934	15.2788	14.9945	15.1944	15.2654	15.4168	15.1252
10	-4.4627	-4.0563	-1.9749	0.6810	2.4754	3.3358	17.7842	17.3248	17.4847	17.7065	17.6840	17.5384

Table III.- Background QTL frequencies with respect to different original marker allele frequencies.

Generation	Flanking markers selection						MBLUP selection					
	0.5/0.05	**0.6/0.4**	**0.7/0.3**	**0.8/0.2**	**0.9/0.1**	**0.95/0.05**	**0.5/0.05**	**0.6/0.4**	**0.7/0.3**	**0.8/0.2**	**0.9/0.1**	**0.95/0.05**
1	0.6180	0.6390	0.6890	0.7341	0.7364	0.7501	0.5679	0.6110	0.6416	0.6933	0.7350	0.7464
2	0.6411	0.7139	0.7652	0.8255	0.8611	0.8932	0.5703	0.6500	0.7043	0.7891	0.8388	0.8750
3	0.6544	0.7283	0.8098	0.8549	0.9199	0.9631	0.6043	0.6646	0.7472	0.8260	0.8863	0.9411
4	0.6664	0.7419	0.8040	0.8786	0.9316	0.9691	0.5911	0.6403	0.7608	0.8541	0.9237	0.9643
5	0.6692	0.7489	0.8306	0.8742	0.9447	0.9763	0.6021	0.6477	0.7801	0.8762	0.9291	0.9719
6	0.7774	0.8217	0.8911	0.9234	0.9805	0.9943	0.6537	0.7080	0.8555	0.9176	0.9586	0.9803
7	0.8333	0.8854	0.9244	0.9531	0.9971	0.9990	0.6962	0.7731	0.8898	0.9421	0.9795	0.9909
8	0.9028	0.9309	0.9588	0.9832	0.9995	0.9995	0.7351	0.8371	0.9182	0.9662	0.9883	0.9969
9	0.9295	0.9644	0.9790	0.9930	1.0000	1.0000	0.7958	0.8708	0.9326	0.9715	0.9888	0.9992
10	0.9524	0.9794	0.9929	0.9962	1.0000	1.0000	0.8321	0.8985	0.9519	0.9838	0.9878	0.9999

Table IV.- Genetic responses for background traits with respect to different original marker allele frequencies.

Generation	Flanking markers selection						MBLUP selection					
	0.5/0.05	**0.6/0.4**	**0.7/0.3**	**0.8/0.2**	**0.9/0.1**	**0.95/0.05**	**0.5/0.05**	**0.6/0.4**	**0.7/0.3**	**0.8/0.2**	**0.9/0.1**	**0.95/0.05**
1	1.9998	2.1432	2.5015	3.2092	4.0407	4.8583	0.8655	1.1534	1.4256	1.9756	2.8530	3.9484
2	2.8432	3.2699	3.5679	4.5311	5.4362	7.3990	1.2336	1.7907	2.3009	2.9621	4.3014	5.9269
3	3.1343	3.6590	3.9975	4.9051	6.2172	8.6092	1.8413	1.8831	2.7817	3.2276	5.0739	6.9144
4	3.0342	3.8634	3.8374	5.0888	6.4353	9.1065	1.6882	1.9837	2.8650	3.5290	5.4377	7.1601
5	3.1083	4.0119	4.1028	5.1936	6.6466	9.3493	1.7404	2.1813	3.1526	3.6748	5.6472	7.4923
6	5.5306	5.7429	5.8044	7.0193	8.5639	11.4938	2.9042	3.4778	4.4579	4.9242	6.9721	8.7405
7	7.2412	7.1919	7.4355	8.7753	10.3473	13.3135	3.9548	4.5762	5.6100	5.9928	8.0647	9.8254
8	9.5666	9.5303	9.7006	10.9129	12.4398	15.5221	5.0398	5.7184	6.5360	7.1086	9.1688	10.9090
9	11.6835	11.8016	12.1039	12.9604	14.5405	17.4347	6.3393	6.6976	7.6411	8.0432	10.1974	11.8616
10	13.6052	13.9095	14.1916	14.8622	16.4019	19.2994	7.2419	7.7167	8.5444	8.8033	11.1255	12.8525

introgression efficiency in basic group was simulantly studied. The results showed that the result of flanking markers for foreground selection was similar with that of van, namely the introgression QTL frequency was increased with the increase of original marker allele frequency in donor, But as for MBLUP selection for foreground selection, introgression QTL frequency did not change with the original marker allele frequency in donor. Even when the original marker allele frequency was very low, very high introgression QTL frequency was still obtained. For example, the original marker allele frequencies in donor and receptor was 0.5/0.5. After athwart cross for 5 generations, introgression QTL frequency still reached 0.9629.

The study found QTL in marker assisted introgression, when the marker allele frequencies in two specific base population, we should using the MBLUP method of foreground selection, because MBLUP method way to ensure a favorable QTL allele marker-assisted not. It will be lost, but also to achieve greater genetic progress.

CONCLUSION

The results showed that as for MBLUP selection, introgression QTL frequency did not change with the marker allele frequencies. Even when the marker allele frequencies in the basic group were very low, the very high introgression QTL frequency was still obtained. Therefore, when the marker alleles are distributed in two basic groups with a certain frequency, MBLUP method is suggested for foreground selection.

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Statement of conflict of interest

Authors have declared no conflict of interest.

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