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Short communication

Restriction fragment length polymorphism markers in relation to quantitative characters

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Summary. A simple consideration of the potential of restriction fragment length polymorphism mapping, as a method of analysing the inheritance of quantitative characters, suggests that there are severe limitations to the utility of this approach.

Key words: Quantitative characters – Polymorphism – Restriction fragment

Introduction

It has been suggested that restriction fragment length polymorphism (RFLP) markers may be useful in mapping and monitoring quantitatively inherited traits (Beckmann and Soller 1983; Soller and Beckmann 1983; Burr et al. 1983). In this laboratory RFLP mapping is being used to study the organization of DNA sequences in the pea genome (Ellis et al. 1984; Domoney and Ellis 1985). The most effective method we have adopted is to analyse the segregation patterns of RFLPs in recombinant inbred lines (Haldane and Waddington 1931; Bennett et al. 1982). The advantage of this technique is that the segregation analysis is essentially non-destructive, because the lines can be maintained indefinitely allowing cumulative mapping. The suggestion of Soller and Beckmann (1983) and Burr et al. (1983) is attractive as an extension of this work. There are however severe limitations to this approach, and which suggest that such an undertaking could only be successful in some very favourable circumstances.

Segregation of a quantitative character among recombinant inbred lines

In a population of 2N recombinant inbred lines, an RFLP marker (alleles P1 and P2), and a gene governing a quantitative character (alleles C1 and C2) are assumed to be segregating. Let us also assume that the gene C does not interact with any other segregating marker in this population, and that the environmental component of the variance of the quantitative character is negligible. Let the mean and standard deviation of the quantitative character in the parental lines be m1, s1 and m2, s2, respectively.

This simple case describes the ideal circumstance for the detection of linkage between an RFLP marker and a gene governing a quantitative character. This can be used as a model to investigate the relationship between s, N and the recombination frequency at a single meiosis (r), between the loci C and P.

The recombination frequency r is related to the fraction (R) of inbred lines which are recombinant between the loci P and C (Haldane and Waddington 1931):

$$R = 2r/(1+2r). \quad (1)$$

This relationship assumes that the lines have been derived by selfing the hybrid derived from the cross of two homozygotes.

Thus $N(1-R)$ lines are expected to be of the P1P1 C1C1 class and NR lines are expected of the P1P1 C2C2 class. Therefore, in the P1P1 class as a whole, the quantitative character will be represented by the values of two superimposed distributions. One is distributed about the mean m1, and the other about the mean m2. The mean (M) of the combined distribution is given by the equation:

$$M = m1(1-R) + m2(R). \quad (2)$$

The variance of the values of the quantitative characters (S^2) about the mean M is:

$$S^2 = s1^2(1-R) + s2^2(R) + (1-R)(m1-M)^2 + R(m2-M)^2. \quad (3)$$

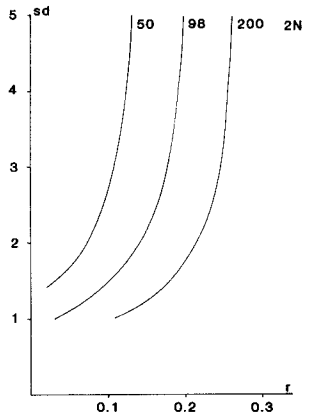

Fig. 1. Relationship between the minimum recombination frequency (r) for which linkage to an RFLP marker can be detected when the parents differ by a given number of standard deviation units (sd). The relationship is shown for different numbers ($2N$) of recombinant inbred lines

If we make the assumptions:

$$s1 = s2 = s, \quad m2 = m, \quad m1 = m + ns .$$

Where n is some constant.

Then equations 2 and 3 can be rewritten:

$$M = m + ns(1 - R) \tag{4}$$

$$S^2 = s^2 + (ns)^2 (R)(1 - R) . \tag{5}$$

Where r = 0.5, R = 0.5 and we get the values:

$$M_{(0.5)} = m + ns/2 \tag{6}$$

$$S^2_{(0.5)} = s^2 + (ns/2)^2 . \tag{7}$$

If linkage between C and P is detectable then M and $M_{(0.5)}$ must be distinguishable, or the condition:

$$2 \geq M - M_{(0.5)} / \sqrt{(S^2 + S^2_{(0.5)})/N} \tag{8}$$

must be satisfied

$$M - M_{(0.5)} = ns(\tfrac{1}{2} - R) \tag{9}$$

$$\sqrt{(S^2 + S^2_{(0.5)})} = s\sqrt{2 + n^2[(R)(1-R) + \tfrac{1}{4}]} . \tag{10}$$

Where $y \geq 2$ we can rewrite (8) as:

$$y = [\sqrt{N}][n(\tfrac{1}{2} - R)] / \sqrt{\{2 + n^2[R(1-R) + \tfrac{1}{4}]\}} .$$

This equation can be evaluated, and for given values of N and n; the minimum value of r which satisfies the condition $y \geq 2$ can be tabulated. This relationship is shown graphically in Fig. 1 for 2N = 50, 98 and 200 recombinant inbred lines.

Conclusions

This simplistic analysis shows that while linkages can be detected between RFLP markers and genes governing quantitative characters under favourable circumstances, it is not appropriate to analyse such linkage in recombinant inbred lines. It would seem that the best strategy for mapping such loci would be to collect sufficient linkage information about a large number of RFLP markers to generate an RFLP linkage map, and then analyse the segregation of these markers in response to breeding selection. However it is difficult to see how this type of analysis could be used to aid a breeding programme because we do not know a priori that the genetic control of a particular quantitative trait will be the same in all genotypes. Furthermore the assumptions which have been made in this analysis are totally unreasonable. For example gene interactions have been ignored, as have the effect of environmental factors on quantitative characters, and this analysis has tacitly assumed that there is no error associated with the measurement of a quantitative character. These three problems combine to suggest that the relationship shown in Fig. 1 is unrealistically optimistic. RFLP markers can really only be used to follow the segregation of reasonably closely linked genes where the segregating alleles confer very different phenotypes (ie classical morphological characters). It is unlikely that they could be useful in the genetical analysis of quantitative characters. The utility of RFLP analysis should not be underestimated, neither should it be misconstrued. RFLP markers can be used to follow the segregation of particular genes of interest, and to analyse cases where segregation cannot be scored without either a complex assay or some backcrossing scheme.

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