Heterosis, maternal effects and Gardner and Eberhart

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1 Abstract

When the parents are grown beside their crosses, the crosses can be compared with the parents: the heterosis of each cross, and Gardner and Eberhart's split of the crosses into variety effects and heterosis. In a diallel with reciprocals, the reciprocal effects split into maternal and non-maternal parts. This vignette takes these three in turn.

2 Heterosis

With the parents grown beside the crosses, `Heterosis()` gives for each cross the heterosis over the mid-parent $MP = (P_i + P_j)/2$, the better parent and, if a check variety is named, the standard variety, in percent, each with a t test. With B replicates the standard errors of the differences are $\sqrt{3MS_E/(2B)}$ for $F_{ij} - MP$ and $\sqrt{2MS_E/B}$ for the other two.

```
het <-
  Heterosis(
```

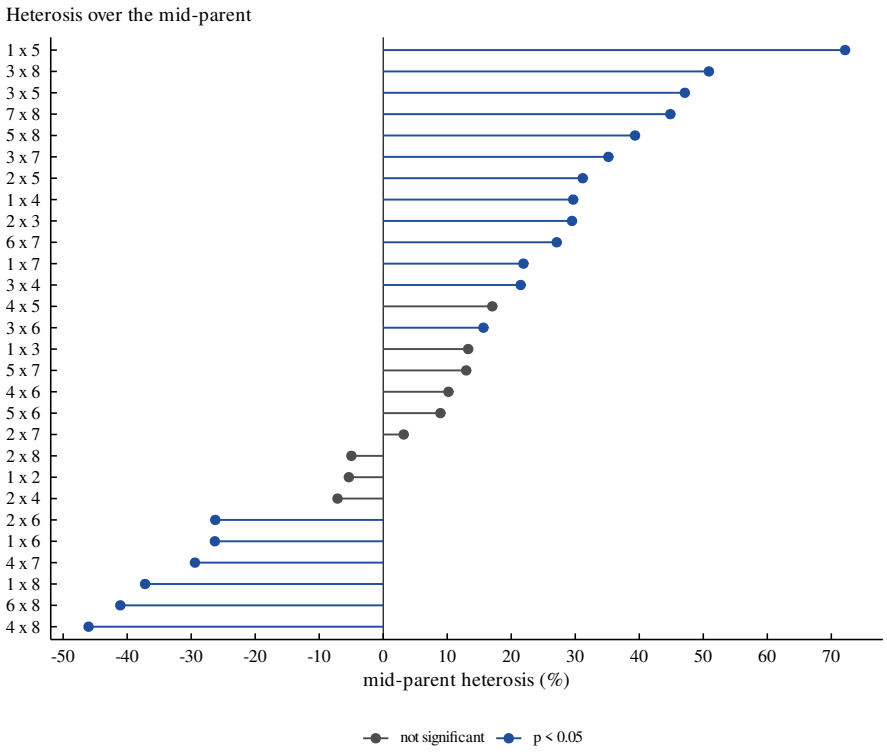
```
      y      = Yield
    , Rep    = Rep
    , Cross1 = Cross1
    , Cross2 = Cross2
    , data   = GriffingData2
    , Check  = 3
    , Better = c("higher", "lower")[1]
    )
het$StdErr
```

```
   F1_MP    F1_BP
6.471663 7.472833
```

```
head(x = het$Heterosis[order(-het$Heterosis$MP)], n = 6)
```

```
   Cross1 Cross2      F1 MidParent BetterParent       MP     t_MP         p_MP
1:      1      5 120.290  69.87375       85.645 72.15335 7.790308 5.025436e-12
2:      3      8 117.735  78.03500       82.000 50.87461 6.134435 1.531526e-08
3:      3      5  94.285  64.08625       74.070 47.12204 4.666304 9.085783e-06
4:      7      8 125.270  86.48000       90.960 44.85430 5.993822 2.926609e-08
5:      5      8  94.820  68.05125       82.000 39.33616 4.136301 7.130931e-05
6:      3      7 111.540  82.51500       90.960 35.17542 4.484937 1.870084e-05
         BP     t_BP         p_BP Check       SH     t_SH         p_SH
1: 40.45187 4.636127 1.025726e-05 74.07 62.40043 6.185071 1.211061e-08
2: 43.57927 4.781988 5.683737e-06 74.07 58.95099 5.843165 5.813966e-08
3: 27.29175 2.705132 7.968289e-03 74.07 27.29175 2.705132 7.968289e-03
4: 37.71988 4.591298 1.227161e-05 74.07 69.12380 6.851485 5.139696e-10
5: 15.63415 1.715547 8.919434e-02 74.07 28.01404 2.776725 6.503853e-03
6: 22.62533 2.753976 6.940153e-03 74.07 50.58728 5.014163 2.174202e-06
```

```
plot(x = het, which = c("MP", "BP", "SH", "residuals", "qq")[1])
```



For traits where a lower value is better (days to flowering, disease score), `Better = "lower"` takes the lower parent as the better one.

3 Maternal and non-maternal reciprocal effects

Cockerham and Weir (1977) write the reciprocal effect of Methods 1 and 3 as $r_{ij} = m_i - m_j + n_{ij}$: a maternal effect of each parent and a non-maternal remainder. `Griffing(..., Reciprocal = "split")` splits the reciprocal line of the analysis of variance accordingly, on $P-1$ and $(P-1)(P-2)/2$ degrees of freedom:

```
rs <-
  Griffing(
      y          = Yield
    , Rep        = Rep
    , Cross1     = Cross1
    , Cross2     = Cross2
    , data       = GriffingData1
    , Method     = 1
    , Model      = 1
    , Reciprocal = c("combined", "split")[2]
```

```
    )
rs$ANOVA
```

```
              Df  Sum Sq Mean Sq F value Pr(>F)
gca            7  3804.6  543.52 18.8868 <2e-16 ***
sca           28 22060.8  787.89 27.3783 <2e-16 ***
maternal       7    77.7   11.10  0.3856 0.9100
non-maternal  21   287.9   13.71  0.4763 0.9758
Error        189  5439.0   28.78
---
Signif. codes:  0 '***' 0.001 '**' 0.01 '*' 0.05 '.' 0.1 ' ' 1
```

```
round(x = rs$Maternal, digits = 3)
```

```
     1      2      3      4      5      6      7      8
 0.087  0.681  0.968  0.830 -0.818  0.196 -1.257 -0.686
```

```
round(x = rs$StdErr[c("mi", "mi_mj", "nij")], digits = 3)
```

```
   mi mi_mj   nij
1.255 1.897 3.285
```

Here neither part is significant: the reciprocal differences of this diallel are small and show no maternal pattern.

4 Gardner and Eberhart's Analyses II and III

For parents and one set of crosses, Gardner and Eberhart (1966) model the parents by variety effects v_j and the crosses by the mean of their parents plus heterosis. Analysis II splits the heterosis into average heterosis $\bar{h}$, variety heterosis h_j and specific heterosis $s_{jj'}$:

```
ge2 <-
  GardnerEberhart(
      y        = Yield
    , Rep      = Rep
    , Cross1   = Cross1
    , Cross2   = Cross2
    , data     = GriffingData2
    , Analysis = 2
    , Model    = 1
    )
ge2$ANOVA
```

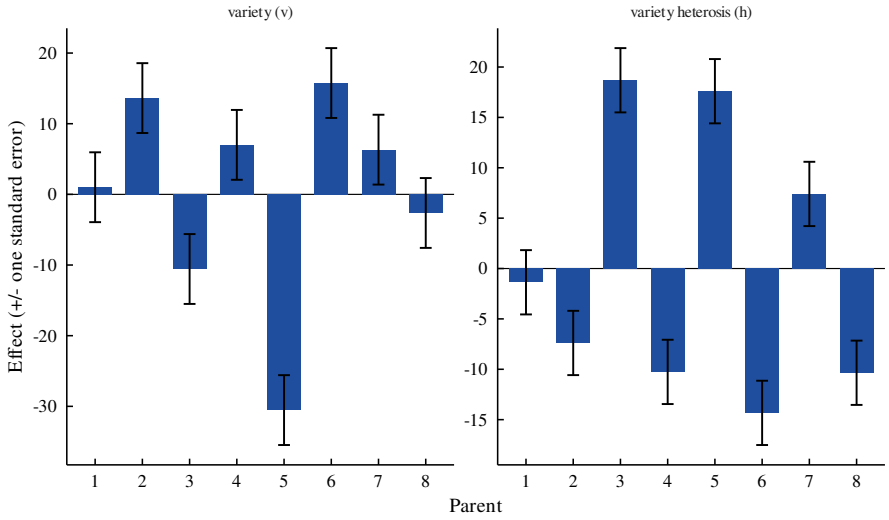
```
                    Df  Sum Sq Mean Sq F value    Pr(>F)
Varieties            7  1850.9  264.41  9.4698 4.546e-09 ***
Heterosis           28 12529.1  447.47 16.0259 < 2.2e-16 ***
Average heterosis    1   373.8  373.81 13.3879  0.000398 ***
```

```
Variety heterosis    7  2850.7  407.25 14.5854 3.807e-13 ***
Specific heterosis  20  9304.6  465.23 16.6619 < 2.2e-16 ***
Error              105  2931.8   27.92
---
Signif. codes:  0 '***' 0.001 '**' 0.01 '*' 0.05 '.' 0.1 ' ' 1
```

```
ge2$Average
```

```
      Estimate Std. Error   t value     Pr(>|t|)
mu_v 84.633437   1.868208 45.301929 9.626013e-71
hbar  7.750938   2.118349  3.658952 3.980309e-04
```

```
plot(x = ge2, which = c("effects", "specific", "residuals", "qq")[1])
```



Analysis III keeps the variety effects for the parents and analyses the crosses by general and specific combining ability, with average heterosis between the two; its gca and sca lines are Griffing's Method 4:

```
ge3 <-
  GardnerEberhart(
      y        = Yield
    , Rep      = Rep
    , Cross1   = Cross1
    , Cross2   = Cross2
    , data     = GriffingData2
    , Analysis = 3
    , Model    = 1
    )
ge3$ANOVA
```

```
                   Df Sum Sq Mean Sq F value    Pr(>F)
Varieties           7 1574.8  224.96   8.057 8.099e-08 ***
Average heterosis   1  373.8  373.81  13.388  0.000398 ***
gca                 7 3126.9  446.70  15.998 3.672e-14 ***
sca                20 9304.6  465.23  16.662 < 2.2e-16 ***
Error             105 2931.8   27.92
---
Signif. codes:  0 '***' 0.001 '**' 0.01 '*' 0.05 '.' 0.1 ' ' 1
```

5 Summary

`Heterosis()` compares each cross with its parents and a check; `Griffing(..., Reciprocal = "split")` asks whether the reciprocal differences come from the mother; `GardnerEberhart()` describes parents and crosses with one model of variety effects and heterosis.

6 References

Cockerham, C. C. and Weir, B. S. (1977). Quadratic analyses of reciprocal crosses. *Biometrics*, 33(1), 187–203.

Gardner, C. O. and Eberhart, S. A. (1966). Analysis and interpretation of the variety cross diallel and related populations. *Biometrics*, 22(3), 439–452.

Murray, L. W., Ray, I. M., Dong, H. and Segovia-Lerma, A. (2003). Clarification and reevaluation of population-based diallel analyses: Gardner and Eberhart Analyses II and III revisited. *Crop Science*, 43(6), 1930–1937.

Singh, R. K. and Chaudhary, B. D. (2004). *Biometrical Methods in Quantitative Genetic Analysis*. Kalyani Publishers, New Delhi.