

MATERNAL AND PATERNAL EFFECTS ON THE OIL CONTENT OF CYPSELA IN F₁ SEED.

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ABSTRACT

The sunflower kernel is mostly embryonic tissue which could be influenced by heterosis if the parents were genotypically different. However, it is generally agreed that the maternal genotype is the primary determinant of oil percentage in the cypselas of F₁ seed. An examination of published data showed that heterosis can affect seed sink size which in turn could produce a 20% increase in the oil content per seed due to pollen genotype. The effect of seed sink size on heterosis in oil content was studied in field experiments. The expression of heterosis was found to be dependent on the complex relationship between sink size as determined by the number of seeds and the supply of photogynthate. When sink size was controlled, heterosis, caused by a wide genetic difference in maternal and paternal genotypes, produced a 77% increase in oil content per seed. Most of this increase was related to an increase in seed size. The implications of these findings to breeding programs and cultivar trials are important. In the presence of insect pollinators, cultivars of low to moderate self compatibility could benefit from heterosis in oil content per seed associated with cross pollination. This would be less likely to occur in a cultivar with a high degree of self compatibility.

INTRODUCTION

The sunflower kernel is almost totally embryonic tissue with little or no endosperm at maturity. Cell division of the fertilised nucleus could be expected to respond to heterosis if the pollen source was genotypically different to the female parent. Constraints placed on the female sink by seed number and size, hull percentage and the potential of the plant to synthesise oil, puts obvious emphasis on the maternal role in determining oil percentage.

Wild and cultivated species of *Helianthus* are well known for their incompatibility (Heiser, 1954). Natural evolution in the wild species favoured cross pollination to achieve good seed fill and this principle was subsequently exploited by man to generate hybrid vigour prior to the development of cytoplasmic male sterility (cms).

Studies of heterosis in sunflowers have concentrated on the contribution of maternal and paternal genotypes on oil percentage. They generally agree that maternal effects are all important but environmental conditions can have a large effect on oil content. However, it is clear that the effect of pollen on the quantity of oil in the seed has received little attention. This paper studies this effect by examining data presented in the literature and then describes experiments designed to evaluate the effect of sink size on heterosis.

LITERATURE REVIEW

Maternal and Paternal effects. The contribution made by the male and female parents to seed weight and oil percentage have been studied over many years. Kushnir (1957, 1958) compared the 1000 seed weight of self and cross pollinated plants of the same cultivar in 2 seasons. Seed from the self pollinated heads were much smaller than the cross pollinated heads which suggests that pollen source affected seed fill. However, Pawlowski (1964) claimed the pollen parent had no effect on the oil content of the maternal genotype. Stoyanova *et al.*, (1974) examined the effect of sib and cross pollination on male fertile inbred lines. Free pollination (44.2%) increased oil percentage more than sibbing (39.3%) when compared with selfed heads (38.6%). Similar results were obtained with kernel weights. In a second experiment the influence of a male parent with a high oil percentage (58.2%) on the oil percentage of female lines with lower values was studied. The average oil percentage in the kernel of the female lines was raised from 46.3% (selfed) to 47.7% (crossed) and it was concluded that the maternal genotype was all important.

The discovery of cms enabled crosses to be made easily and Harada and Miller (1978) showed that the presence of male sterile cytoplasm in females did not influence oil percentage of kernels, and concluded that it was controlled by the genotype of the female. Sindagi (1976) crossed two different pollen parents with four cms females of varying oil percentage. He found traits such as oil percentage and weight of seed were influenced by the pollen parent which could increase oil percentage by 15% (mean of hybrids of the two pollen parental lines) when compared with the cms female fertilised with its own B line pollen (Table 1). However, when the data was recalculated for oil content (mg oil/seed) there was a 24% increase due to the pollen parents which was considerably larger than the increase in oil percentage caused by the pollen parent. Furthermore, the rankings in oil content when compared with oil percentage were reversed for RHA 266 and RHA 274 and also for CMS 124 and CMS 234.

Table 1. Percentage oil and oil content per seed in parental lines and crosses in F1 seed (after Sindagi, 1976).

| Line | Female (cms)* | Pollen parent RHA 266 Oil % | Pollen parent RHA 274 Oil % |
|--|---------------|-----------------------------------|-----------------------------------|
| CMS 2 | 28.9 | 32.2 | 30.2 |
| CMS 204 | 32.8 | 33.9 | 42.0 |
| CMS 124 | 39.3 | 46.2 | 51.1 |
| CMS 234 | 43.9 | 52.4 | 46.0 |
| Mean | 36.2 | 41.2 | 42.3 |
| Oil content (mg seed ⁻¹) | | | |
| CMS 2 | 18.3 | 22.2 | 20.7 |
| CMS 204 | 18.1 | 24.0 | 24.5 |
| CMS 124 | 26.2 | 32.3 | 31.2 |
| CMS 234 | 23.5 | 31.0 | 27.3 |
| Mean | 21.5 | 27.4 | 25.9 |
| Line 1000 seed wt. Oil content (mg/seed) | | | |
| Note: Parental Values | RHA 266 | 37.4 | 12.7 |
| | RHA 274 | 29.5 | 10.4 |

*Maintained with its B line.

Thompson *et al.*, (1979) showed that the pollen parent had no significant effect on oil percentage when pollen from maintainer (B) lines was used to cross cms (A) lines in all combinations. Two of the lines were oilseed types and two were non-oilseed types. The experiments were carried out at Bushlands and Fargo and at both sites the genotype of the maternal parent controlled oil percentage (Table 2). However,

the maternal and paternal genotypes interacted in their effect on seed weight. At Bushland, the oil content per seed was increased by 33% when compared with the A line pollinated with its maintainer line. However, at Fargo, the data varied considerably (200 seed weight as low as 1.8 g for one combination) due to specific genotype and environment interactions.

Table 2. Effect of maternal and paternal parents with high and low oil percentage on seed characteristics in F1 seed (after Thompson *et al.*, 1979).

| Site and Seed Characteristics | Maternal-High Oil | | Maternal-Low Oil | |
|----------------------------------|-------------------------------|-------------------|--------------------|------------------------------|
| | Pollen-High Oil Maintainer | Pollen-Low Oil | Pollen-High Oil | Pollen-Low Oil Maintainer |
| Bushland | | | | |
| Oil (%) | 41.0 | 40.7 (99)† | 24.8 (109) | 22.8 |
| 200 seed wt(g) | 13.4 | 15.7 (117) | 21.9 (122) | 17.9 |
| Oil Content (mg/seed) | 28.0 | 32.0 (114) | 27.1 (133) | 20.4 |
| Fargo | | | | |
| Oil (%) | 39.6 | 41.2 (104) | 29.2 (97) | 30.2 |
| 200 Seed wt(g) | 12.1 | 13.0 (107) | 12.5 (67) | 18.7 |
| Oil Content (mg/seed) | 23.9 | 26.7 (112) | 18.2 (66) | 27.5 |

† value expressed as a percentage of the cms and maintainer.

Relationship between seed weight and percentage oil. No consistent conclusions have been reached by the many authors who have studied the relationship between seed weight and oil percentage. Skoric (1974) found a negative, but non significant correlation in heterogenous F1s of 4 open pollinated (O.P.) cultivars. This was confirmed by McWilliam *et al.*, (1978) in another O.P. cultivar (Sunfola 68.2, an Australian selection of Peredovik). Russell (1953) studied homozygous inbred lines and their heterozygous top crosses. A significant negative correlation was found with the inbreds but not in the top crosses. Fick (1973, 1974) confirmed that a significant negative correlation of oil percentage with seed weight occurred in inbreds, small seeds giving higher oil percentages. In his second study, he found higher variances in oil percentage among seeds within the heads of O.P. cultivars than in the inbred lines. This suggested that the genotype of the pollen may have some influence on the oil percentage of the seed.

In summary, it appears that if the degree of heterogeneity of the population is sufficient, a negative relationship exists between seed weight and oil percentage of the kernel.

Environmental effects. The influence of environmental conditions on the oil percentage and yield of seed is apparent in trials comparing commercial oilseed cultivars. Fifteen oilseed cultivars were grown at 5 sites in Australia in 1980 (Frame 1981). Variability in oil percentage between sites (35.3 to 45.0) was much greater than the variability between cultivars (38.4 to 40.9). Similar results were shown in National trials in the USA where 28 cultivars were

compared. The mean oil percentage for the sites ranged from 39.4 to 49.4 but the standard deviation in oil percentage between cultivars at each site was less than 2.2%. The commercial cultivars would be genetically uniform and crossing between lines would depend on the level of self compatibility and incidence of pollinators.

These results show that heterosis caused by the pollen parent expressed as oil percentage is small but the effect on oil content per seed is often overlooked. In fact, the increase in oil content per seed calculated from published data is frequently larger than that shown in oil percentage. There is some evidence that sink size or environmental constraints such as water and nutrient stress during seed development may have influenced the full expression of heterosis.

EXPERIMENT 1

Methods. This experiment was carried out to study heterosis in a range of cultivars showing varying degrees of self compatibility. An open pollinated and five hybrid cultivars available commercially were sown in the field at Griffith in 1980. A split plot design was used and the heads were allowed, or not, to cross pollinate by the use of insect-proof cages.

The traits measured included seed weight, kernel weight, seed volume, ratio of kernel to seed (kernel percentage), oil percentage in the seed and kernel and oil content. Total oil percentages were determined with the Newport NMR analyser.

Results. Self compatibility ranged from 21% (cv 1) to 100% (cv 4) (Table 3). The pollination treatments and varieties significantly interacted ($P < 0.01$) in their effect on seed set, seed weight, oil percentage and oil content. The cultivars with low self compatibility (e.g., cv 1 and 5) had significantly larger seed when cross pollination was prevented. Inside the cage, the sink size in both of these cultivars was restricted by the small number of seed fertilised and this

resulted in a reduced oil percentage when compared with the same cultivar growing outside the cage.

The oil content per seed in cultivars with moderate compatibility (e.g., cvs 2, 3) was 32% higher outside the cage and was mainly due to larger seed (25% larger) rather than higher oil percentage (7% higher). This was despite the larger sink size in the plants growing outside the cage.

Table 3. The effect of pollen source on four traits with six cultivars of varying self compatibility.

| Cultivar | % seed set (full seed) | 1000 seed weight (g) | total oil (%) | oil content (mg/seed) |
|--------------|---------------------------|-------------------------|------------------|--------------------------|
| Inside cage | | | | |
| 1 (O.P.) | 16.3 (21) † | 72.9 | 41.5 | 30.1 |
| 2 (HYBRID) | 49.9 (73) | 36.2 | 37.7 | 14.1 |
| 3 (HYBRID) | 59.0 (78) | 35.8 | 43.9 | 15.6 |
| 4 (HYBRID) | 68.9 (100) | 49.3 | 49.3 | 24.3 |
| 5 (HYBRID) | 42.3 (55) | 59.8 | 42.6 | 25.4 |
| 6 (HYBRID) | 70.1 (95) | 33.3 | 44.5 | 14.9 |
| Mean | 51.1 (70) | 48.0 | 43.2 | 20.8 |
| Outside cage | | | | |
| 1 (O.P.) | 76.1 | 56.9 | 49.9 | 28.4 |
| 2 (HYBRID) | 68.7 | 46.5 | 41.8 | 19.5 |
| 3 (HYBRID) | 75.6 | 43.1 | 47.0 | 20.2 |
| 4 (HYBRID) | 68.6 | 53.6 | 48.3 | 26.0 |
| 5 (HYBRID) | 77.5 | 37.8 | 44.1 | 17.2 |
| 6 (HYBRID) | 74.0 | 40.4 | 46.5 | 18.9 |
| Mean | 73.4 | 46.3 | 46.3 | 21.7 |
| L.S.D. 5% | 4.7 | 4.6 | 1.4 | 2.0 |

† seed set as % of freely pollinated (outside cage).

EXPERIMENT 2

Methods. This experiment was designed to compare the contribution of the pollen genotype to heterosis under conditions of similar sink size.

AHA 89, a cms female of good combining ability was chosen. Half of each capitulum was crossed with its own B line pollen and the other half was crossed with genetically different SIROSUN (CSIRO) restorer pollen. This allowed maximum heterosis.

Bags were used to cover the heads before, during and after pollination and to collect pollen. Pollinations by foreign pollen or its own pollen were made each day as disc florets become progressively fertile towards the centre of the

capitulum. The same traits were measured as in Experiment 1. The two treatments were replicated on sixteen heads.

Results. The pollen treatments had no significant effect on the number of seed set (Table 4). The restorer line pollen significantly increased the oil percentage by 16% and the seed weight by 58% when compared with AHA 89 pollinated with its genetically similar maintainer line. This resulted in a highly significant ($P < 0.01$) increase of 77% in oil content per seed.

Table 4. Effects of SIROSUN restorer pollen compared to B line pollen of the cms female AHA 89.

| Trait | Pollen Source | | L.S.D. 1% |
|---------------------------------|----------------------|--------------------|-----------|
| | Maintainer B line | Restorer R line | |
| Seed set (numbers/half head) | 369 | 388 | n.s. |
| 1000 seed weight (g) | 45.5 | 71.8 (158) * | 15.1 |
| Total oil (%) | 39.1 | 45.2 (116) | 2.9 |
| Oil content (mg/seed) | 17.9 | 31.6 (177) | 6.6 |

n.s. not significant

* as percentage of Maintainer B line

DISCUSSION

Research on heterosis in F₁ seed has concentrated on oil percentage with less attention paid to seed weight and oil content. In National Variety Trials, the variability in oil percentage within commercial oilseed cultivars at the one site is relatively small whereas there is often a large variation in oil percentage between sites. This, presumably, is because different environmental conditions between sites influence sink size and the supply of photosynthate. The complexity of the relationship between sink size and heterosis was demonstrated in Experiment 1. However, the results did show that in uncontrolled cross pollination in cultivars of moderate compatibility, greater heterosis was exhibited in oil content per seed than in oil percentage. Under the conditions of

similar sink strength in Experiment 2, the pollen genotype made a significant contribution to heterosis in F₁ seed as shown in oil percentage, seed size and oil content per seed.

In the design of experiments to detect heterosis, parental lines with large differences in oil percentage, but with small differences in seed weight were chosen. The use of a cms female line in the second experiment, prevented self pollination. The heterosis measured in these experiments is likely to be much greater than in commercial cultivars because of the choice of material.

The final yield of a crop is determined by the oil content per seed, number of seeds in the capitulum and the number of capitula per unit area. In small plot trials, the yield of cultivars

with moderate to low self compatibility may be enhanced when compared with highly self compatible cultivars. Cross pollination by insect pollinators would be favoured in cultivars with moderate to low self compatibility whereas cross pollination would be less likely in a highly self compatible cultivar. The possibility may exist for the yield of commercial crops to be increased by sowing two cultivars with similar maturity but of moderate to low self compatibility rather than one cultivar.

The contribution made by the maternal genotype to heterosis is well established. The study shows that the pollen genotype can make a significant contribution to reproductive heterosis in some traits, particularly oil content per seed.

ACKNOWLEDGEMENTS

Assistance in computations and manuscript by Dr W.A. Muirhead (CSIRO Division of Irrigation Research) and oil analysis by Mr A.D. Johnson (CSIRO Division of Tropical Crops and Pastures) are greatly appreciated. Thanks are also due to Mr P. Pistillo for help in carrying out the trials.

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T1982GEN16

GENETIC EFFECTS OF DAYS TO FLOWERING IN SUNFLOWER (*HELIANTHUS ANNUUS* L.) UNDER SHORT DAY REGIME.

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ABSTRACT

Four genotypes of sunflower, *Helianthus annuus* L., with diverse flowering dates were crossed in a partial diallel. These four parental lines, F₂ progeny, F₂ progeny from reciprocal crosses, and backcross F₁ progeny of these crosses were planted in a randomized complete block design at Molokai, Hawaii, the winter of 1981. The number of days were recorded from the time sunflowers were planted to when 50 percent were in flower. Genetic effects were estimated. Additive effects were statistically significant while dominance, epistasis, and reciprocal effects were all nonsignificant. Estimated heritability coefficient of 39.8 percent was determined indicating moderate success in selecting for different flowering dates.

INTRODUCTION

Information concerning the inheritance of the number of days from planting to flowering in sunflower, *Helianthus annuus* L., is limited and somewhat conflicting. Unrau (1947) and Putt (1965) reported overdominance in F₁ progeny of certain crosses where the F₁ progeny flowered earlier than either parent. Kovacik and Skaloud (1978) reported different

genetic effects when they divided the period from planting to flowering into two phases: 1) from planting until 'head setting' (presumably budding), and 2) between head setting and florescence (bud to flowering). They found additive genetic effects predominating in phase one and dominant effects predominating in phase two. Fick (1978) reported isolated lines from the cultivar 'Volgar' which segregated for early and late flowering plants with early flowering conditioned by a single recessive gene.

Reported estimates of heritability for days to flowering have been quite high. Shabana (1974) reported broad sense heritability of 97.7% and Russell (1953) reported heritability estimated by correlation coefficients of 0.86 and 0.91 between days to flowering of certain inbred lines and their top cross progeny.

This is a preliminary report of a study to define genetic effects and inheritance of days to flowering and of photoperiod on flowering for certain sunflower parental lines and segregating progeny from diallel crosses.