size. Each plant, therefore, has many blossoms and early developing fruits throughout the harvest period. Using the controlled environment studies as a model we would assume that these plants would have a high transpiration rate and good leaf development. The high water use measured during harvest in our lysimeter studies support this assumption.

We do not know what caused the increase in transpiration rate of cucumbers, however, recent research with excised barley leaves (6) and tobacco (9) showed increased transpiration associated with higher gibberellin and cytokinin levels. We feel that growh regulator levels in the rapidly dividing, highly metabolic cells of young cucumber fruits should be investigated as an underlying cause of the increased transpiration rate.

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Compositional Changes in Muskmelons during Development and in Response to Ethylene Treatment¹

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Additional index words. Cucumis melo, cantaloupe, Honey Dew, fruit ripening, sugars, soluble solids

Abstract. Fruits of muskmelon (Cucumis melo L., cv. Honey Dew and Powdery Mildew Resistant No. 45) were harvested at weekly intervals after anthesis, and weight, shape, flesh firmness, flesh color, and the content of total solids, alcohol insoluble solids, total sugars, reducing sugars, glucose, fructose, and sucrose were measured. Total sugars (mainly sucrose) increased rapidly between the 28th and 42nd days; hence early harvest must inevitably lead to loss in quality. Ethylene treatments of fruits harvested less than fully mature did not alter sugar content since melons have no starch reserve.

Muskmelons are among the sweetest of the fleshy fruits. For example, in this laboratory, we have found soluble solids contents (SSC) as high as 17% of the juice in fully ripened 'Honey Dews'. The sugar contents of ripe melon fruits have often been reported (frequently as SSC), but there have been few reports of sugar analyses in relation to stages of fruit development. Pratt (16) reviewed the biochemistry of melon fruits and made the following points: Sugar accumulation during the development of muskmelons is of special interest, since sugar content is used by many as the principal criterion of fruit quality, not only in research and in commerce but also in enforcement of marketing regulations. Many workers have shown a strong correlation between high SSC and other attributes of high quality. Sugar content and cultural practices have been related in many reports which can be readily located in the literature; in general it appears that the highest sugar contents

will be found in melons on healthy vines with a high yield. In more recent work (1, 24) it has been pointed out that high SSC alone does not adequately define good melon quality. The best flavor depends on "sweetness," which is only partially correlated with SSC, and on ideal proportions of various volatile compounds whose nature is not yet fully defined. Nevertheless, while all melons with high SSC will not necessarily be of good quality, the absence of high SSC makes good quality very unlikely (24).

In this work we followed changes in various sugar-related components of 2 important muskmelon types from early stages in fruit development to maturity. We hoped to correlate changes in sugar content with other changes in the physical characteristics of the fruit, so as better to understand physiological criteria for the commercial harvesting of muskmelons. Because 'Honey Dews' are regularly treated with ethylene during commercial handling, the effect of ethylene treatment on melon composition was also examined.

Materials and Methods

Plant material. The muskmelon cultivars studied, 'Powdery Mildew Resistant Cantaloupe No. 45' ('PMR-45') and 'Honey

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Dew', differ in many respects (2). 'PMR-45' is a typical netted "cantaloupe" type with orange flesh; it abscises from the vine upon reaching maturity. In commercial practice such fruits are described as "full slip." 'Honey Dew' is a smooth-skinned pale vellow melon with green flesh; it usually remains attached to the vine until commercially overripe. The fruits used in these studies were grown on the University of California farm at Davis in rows 3 m apart. When the first 2 leaves were well-formed, the plants were thinned to a 1 m spacing in the row. Irrigation by furrows was applied as needed. Fertilizer was applied as follows (per 100 m row); 2.25 kg ammonium phosphate before planting and 8.67 kg ammonium sulfate at thinning. Pistillate flowers were tagged at anthesis (13), and the no. of fruits set on each day determined 6 days later. Sufficient 'PMR-45' fruits were set on July 4 in a row planted on May 15 for the purpose of this study. The experimental 'Honey Dew' fruits were set on July 11 in a row planted April 22. Ten fruits of each kind were harvested each week after anthesis, and all data obtained are referred to in terms of fruit age (e.g. 7-day fruit refers to fruits tagged at anthesis and harvested 7 days later). Collection of data was started at 7 days because most cantaloupe fruits that fail -to set can be distinguished by this age (10), and it has been shown that cell division in 'Honey Dew' was completed within 5 days after anthesis, so subsequent growth is primarily due to cell enlargement (11). Sampling continued until abscission occurred in the cantaloupes and until the 'Honey Dew' fruits were fully ripe on the vine.

Fruit growth. The harvested samples were weighed and measured. Shape was recorded as the ratio of polar to equatorial diameters, so the higher the observed ratio the more elongate is the fruit.

Flesh properties. Firmness was determined as the average of 3 readings on a 4 cm equatorial slice from each melon, using a penetrometer (Ametek mechanical force gauge, Model 1-30-M) with a 0.5 cm² plunger. Pressure was expressed in grams required to force this plunger into the center of the pericarp in a direction paralleling the axis of the fruit at the points of attachment of the placentae. Color was measured with an Agtron reflectance spectrophotometer (Model M-400) using a homogenate prepared from the interplacental flesh of the same transverse slices (50 g tissue blended with 50 ml distilled water).

Flesh analyses. All analyses were carried out on the interplacental pieces from the equatorial slices described above: 5 mm of skin and outer cortex was pared from each piece (only 3 mm in 7-day fruits), and the remaining tissue was chopped into small pieces and thoroughly mixed. For total solids, 20 g of tissue were freeze dried, and the weight of dry tissue was expressed as % of fresh wt, as were the results of the other analyses detailed herewith. For sugar determination, 50 g of tissue were blended with 100 ml of 80% ethanol, the homogenate was decanted, and the blender cup rinsed with a further 50 ml of ethanol; the mixture was stored at 00 until analyzed. Before analysis, all samples were filtered and the solutions made up to 500 ml with 80% ethanol; all analyses were performed in duplicate. Total sugars were determined colorimetrically by the method of Dubois et al. (4) and reducing sugars by the method of Somogyi (22). Glucose was determined by a modification of the glucose oxidase-peroxidase system (9, 23) using 75 ml water, 8 ml of 1 M K₂HPO₄, 17 ml of 1 M KH₂PO₄, 4 mg glucose and oxidase (B grade of C. F. Boehringer, 45 EU/g), 5 ml horseradish peroxidase (1 mg/ml of Sigma type II, 135 purpurogallin units/mg), and 1 ml dianisidine (0.8%). A test tube containing 2.5 ml of this reagent and 1 ml of appropriately diluted alcoholic sugar solution was incubated 30 min at 370 in a water bath. The absorbance of this mixture was measured at 420 mu using a Spectronic 20 (Bausch and Lomb) spectrophotometer. Sucrose was calculated as the difference between total sugar and reducing sugar contents, and fructose was calculated as the difference between reducing sugar and glucose contents. Alcohol

insoluble solids (AIS) were determined by drying the residue insoluble in the 80% ethanol sugar extraction at 80° for 24 hr.

Ethylene treatment. Forty fruits of the same setting date were harvested in the morning when the flesh temp was close to 20°C, and subsequent operations were conducted at this temp. Fruits of 'PMR-45' were harvested on July 31 at 28 days after anthesis; cantaloupes of this age are less than full size but have achieved many physiological characteristics of maturity (21). The 'Honey Dew' fruits were harvested on August 22 at 42 days after anthesis; fruits of this age are well-matured but have not yet started self-ripening (17). The samples were matched into 4 lots; 1 lot was analyzed immediately by the methods described above, and the other fruits were placed singly in respirometer jars through which humidified air was passed at a rate to hold the effluent CO2 concn below 0.5%. Ethylene at 60 ppm was administered to half the melons by the continuous flow method of Pratt et al. (18). The respiration rate was determined by gas chromatography. Each day thereafter, 10 treated and 10 control fruits were withdrawn for analysis.

Results

The results of this study are summarized in Fig. 1 and 2; most of the analytical results are in terms of % composition on a fresh wt basis. Assuming that the whole fruit will have a composition reasonably close to that of the flesh sampled, we recalculated these data to give the curves of Fig. 3 in terms of total accumulation of substance in the growing fruits.

Fruit growth. Cumulative growth expressed as fresh wt (Fig. 1 and 3) followed the sigmoid curve expected in determinant plant organs and which has been shown by other investigators of melon fruits (16). PMR-45' grew more slowly at first than did 'Honey Dew', but after 21 days its growth rate was essentially linear until the fruit abscised; it is particularly interesting that this fruit continues to grow actively as long as it is attached to the vine (13). 'Honey Dew' grows much more rapidly than 'PMR-45' for about 6 weeks, but 35-day fruits have achieved almost their maximum size and wt; these fruits may remain attached to the vine for more than 56 days (11, 12). Both 'PMR-45' and 'Honey Dew' were initially oblong, but by 21 to 28 days their final more nearly spherical shape was attained (Fig. 1), results which agree closely with the data of others (3, 11).

Flesh color. In 'PMR-45' the green/red ratio decreased linearly, reflecting the changing balance between the contents of chlorophyll and carotenoids in the flesh (19). Very little carotene is found in 'Honey Dew' (7), and flesh color changed very little after 14 days (Fig. 1).

Flesh firmness. In 'PMR-45' softening began after 28 days and proceeded rapidly; further softening takes place, of course, as these melons ripen after harvest. Softening began after 35 days in 'Honey Dew' and was much more rapid after 49 days when the fruit was becoming overripe (Fig. 1).

Total solids (dry wt). The solids content in terms of % composition shows little change during the period of most rapid fruit growth (Fig. 1), since increased size reflects both dry wt increase and water uptake. Actually the total accumulation of solids in the flesh is rapid and almost linear from day 7 to the end of fruit development (Fig. 3). As growth slows the solids content of the tissue can increase, so the most rapid increase in solids percentage occurs from 28 to 42 days; 'PMR-45' then abscises, and 'Honey Dew' shows a slower rate of solids increase. The increases in total solids are primarily due to sugar accumulation.

Alcohol insoluble solids. The total amount of AIS (starch, cellulose, etc.) increased rapidly between 7 and 28 days, increasing more slowly thereafter (Fig. 3). In terms of percentage of total fresh wt, the content dropped in both cultivars, leveling off at about 1% at 21 days (Fig. 1). The rapid, early increase in total amount of AIS must primarily represent the

increase of total cell structural materials during early growth the amount of starch present being very small (7). Conversely, the rapid decrease in the percentage of AIS on a fresh wt basis represents rapid water uptake. After 21 days there is little further change (on either basis); after this time the major components of wt increase in melons are water and sucrose which seem to increase in rough proportion.

Sugars. The pattern for changes in percentage of total sugars in these 2 cultivars almost exactly paralleled the pattern for content of total solids (Fig. 2). There was little change in concn up

to 28 days, but a rapid rise followed until the fruits reached full size at about 42 days. It was particularly noteworthy that almost half of the final concn of sugar in 'PMR-45' was achieved in the last week before abscission. Reducing sugar concn changed very little in 'PMR-45'; there was a slight rise to 35 days followed by a fall during the final week. The principal reducing sugar change was in the glucose content, fructose remaining relatively constant. Sucrose, however, increased very rapidly after 28 days, and the sucrose/reducing sugar ratio increased after 35 days; these changes are reflected in the total

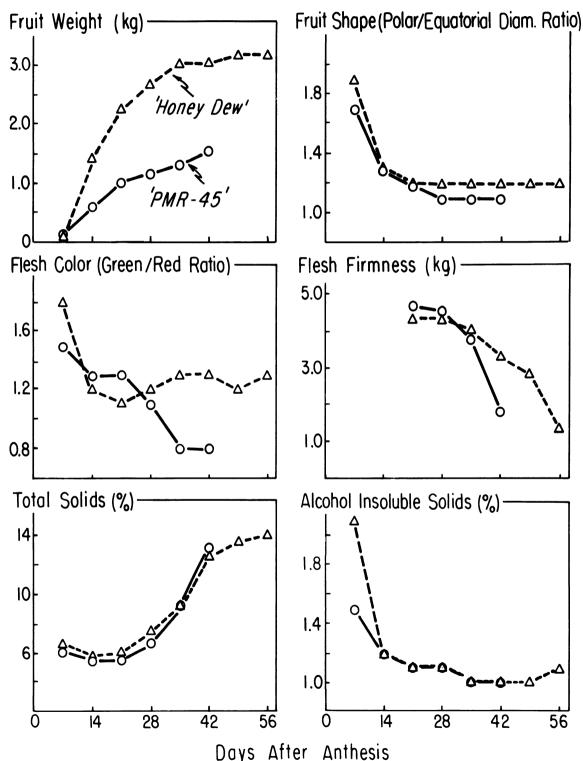


Fig. 1. Changes in muskmelon characteristics as a function of fruit age. Each point is the average of 10 fruits. The symbols are uniform for all graphs.

sugar content of the fruits. In 'Honey Dew' both kinds of reducing sugar increased appreciably to 42 days (full size) and then substantially declined. Sucrose increased steadily between 28 and 49 days, and was still increasing, but more slowly, during the final week. However the final sucrose concn was no higher in 'Honey Dew' than in 'PMR-45' in these samples. Since both kinds of reducing sugar were higher in 'Honey Dew' than in 'PMR-45', the sucrose/reducing sugar ratio showed relatively

little change. The ratio of glucose to fructose dropped rather steadily during the life of 'Honey Dew' but stayed relatively constant until the final week in 'PMR-45'. It is interesting that, while the total sugar content of our 'Honey Dew' samples was higher than in 'PMR-45', the sucrose content was appreciably less.

Response to ethylene. As expected, ethylene treatment induced the respiratory climacteric in both kinds of muskmelon,

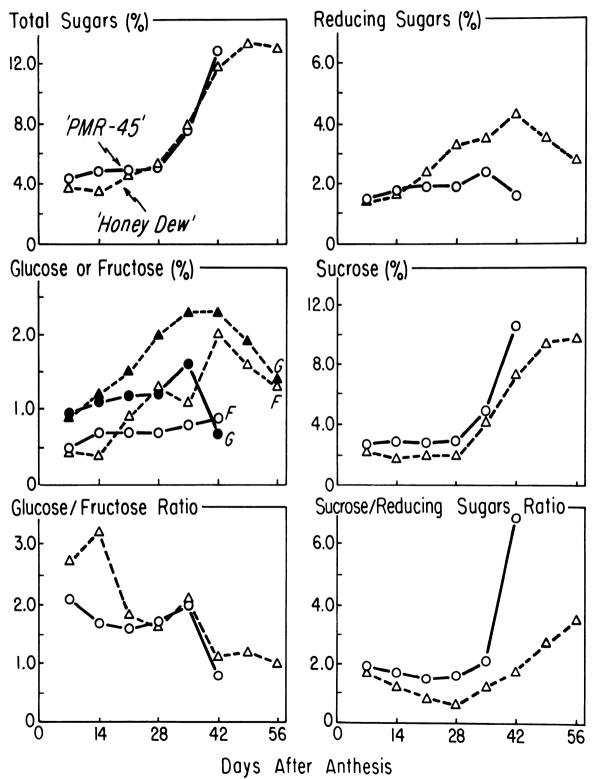


Fig. 2. Changes in sugar contents of muskmelons (expressed as % fresh wt) as a function of fruit age. Each point is the average of 10 fruits. The symbols are uniform for all graphs.

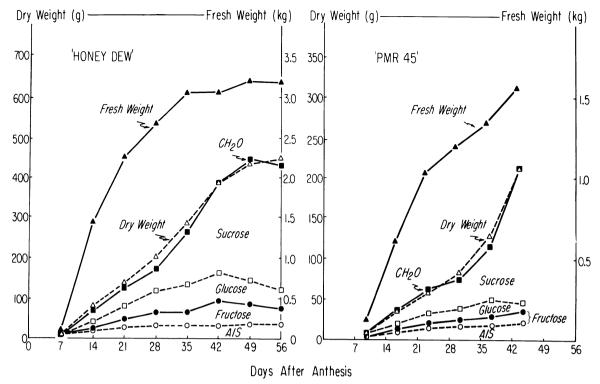


Fig. 3. Changes in total amounts of various carbohydrate components of muskmelons as a function of fruit age, the data being calculated from those of Fig. 1 and 2. The area between each pair of curves represents the portion of the total dry weight attributable to the specified component. The difference between the dry wt curves and the curves from summation of alcohol insoluble solids plus sugars (CH₂O) represents any undetermined sugars and any analytical error. The fresh wt curves are from Fig. 1. Note that the scales for the 'PMR-45' and 'Honey Dew' curves differ by a factor of 2

while the respiration rate declined gradually in the controls (Fig. 4). Softening of the flesh of treated melons was rapid, that of 'PMR-45' finally being too soft for ideal eating, a state which is attained at about 1800 g in our test. Treated cantaloupes developed an external appearance similar to full slip fruit and the red component of the flesh color increased. Treated 'Honey Dew' fruits reached the appearance of vine-ripe fruits in 72 hr while the controls showed no change in superficial appearance; no change in flesh color occurred in either treated or control fruits. There were no significant differences due to treatment in either cultivar in % content of total solids, total sugars, AIS, or reducing sugars. We attribute the small differences shown on the graphs to sampling and analytical variability. The observed changes in fructose and glucose content of treated fruits are significant and reflect those to be expected in the ultimate ripening of untreated fruits (Fig. 2). Sucrose contents showed a slight increase during the experiment but there was no effect of ethylene.

Discussion

The results of our sugar determinations resemble those reported by others (9, 14). Masuda and Kodera (12) studied 'Honey Dew' but, although their fruits were very small, our results for changes in percentage of reducing, nonreducing, and total sugars are in general agreement with theirs. Masuda and Hayashi (11), made a very detailed study of the growth of 'Honey Dew' fruits, and our results agree with their weight and shape data (16). Davis et al. (3) studied fruit growth and development in 'PMR-45' and made many statistical correlations of various characteristics; our growth and total sugar data are similar to theirs. With a semiquantitative method using paper chromatography, Eguchi and Fujieda (5) showed that sucrose was the principal sugar of several muskmelon cultivars. Fruc-

tose and glucose contents were relatively constant, but sucrose accumulation was rapid after about 4 weeks.

Rosa (20) examined the development of several muskmelon cultivars, including 'Honey Dew'; our results agree with his in general, but his sugar values are much lower. He used a different cultivar of cantaloupe, but we cannot explain his lower values with 'Honey Dew', since his total solids data agrees well with ours. We suspect that his 'Honey Dew' melons were untypical of the cultivar at its best, as he was using a late season planting—his melons were ripening about 64 days after anthesis in late Sept. More recent work has shown that late-season melons do not ripen well and are poorer in quality (17). For example, Rosa's 'Honey Dews' reached 10% soluble solids at about 44 days, but we normally expect this value to be reached at 35 days. We have no way of knowing the condition of his melon vines, but it is well known that vines in poor condition produce melons low in sugar (6, 15).

The demonstration that a large part of the sugar (notably sucrose) found in a mature cantaloupe enters the fruit during its last week has important consequences for the industry. Obviously harvesting before full slip or the introduction of any practice which might prematurely detach the melon from the vine (such as spraying with ethephon) will have detrimental results on quality. The sugar present in the fruits at maturity and after ripening has been translocated into the fruit from the vines, since muskmelon cultivars have only insignificant amounts of starch (7, 20). Analysis of our data shows that more than 97% of the total solids in maturing melons of both kinds is in the form of sugar.

Flavor of cantaloupe appears to relate closely to the final rise in sugar content as melons picked earlier than full slip not only are less sweet but never develop good cantaloupe flavor. In 'Honey Dew' this appears to be less important, since these

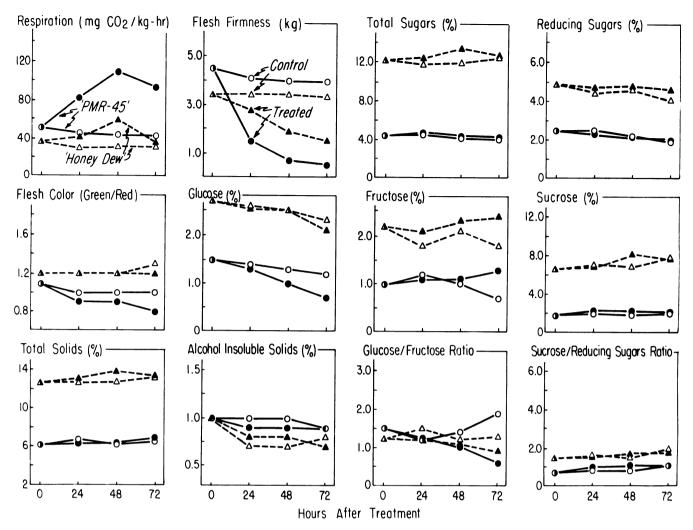


Fig. 4. Changes in characteristics of 28-day cantaloupe and 42-day 'Honey Dew' melons in response to ethylene treatment. Each point is the average of 10 fruits. The symbols are uniform for all graphs, and the scales are the same as for corresponding measurements in Fig. 1 and 2.

melons are mature enough to be of good quality with as little as 10% soluble solids (the requirement of the California Agricultural Code), providing they are ripened with an adequate ethylene treatment (17).

While treatment of unripe fruits with ethylene induces many characteristics of ripe fruit, it will not produce quality where none exists in terms of adequate sugar content, and there is no reserve of starch which can be converted to sugar under the influence of ethylene. Rosa (20) reported an increase in sucrose in 'Honey Dew' melons treated with ethylene during 10 days of storage period, but his melons were picked 45 days after anthesis "... in a decidedly immature condition." Our 42-day 'Honey Dews' were well matured melons of good quality.

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Estimation of Heritability and Combining Ability for Fire Blight Resistance in Pear¹

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Abstract. Heritability estimates for fire blight resistance in pear were obtained by regressing progeny means on midparental phenotypes. Approximately half of the variability in resistance in pear was additive ($h^2 = 0.52$), but there was also evidence for nonadditive genetic effects compatible with a proposed qualitative gene for sensitivity. A method was established to estimate relative average combining ability for fire blight resistance. Progeny means of individual parents were adjusted to the grand progeny mean of 8 intercrossed testers based on common progeny.

Resistance to fire blight, caused by the bacterium Erwinia amylovora (Burrill) Winslow et al., is a major objective of various pear breeding programs in North America. The expression of resistance depends on interactions between the pathogen, host, and environment. Considerable variability in resistance exists, both within and between species (6, 17, 18, 23). Previous studies have suggested that resistance is controlled by both quantitative and qualitative factors. Evidence for dominant factors for both resistance (14, 21) and sensitivity (20) have been postulated, and numerous studies have noted considerable variability between parents in their ability to transmit resistance to their offspring (14, 15, 21, 23).

Estimation of heritability and combining ability are related techniques that describe the nature of genetic variability in a population and that are useful for selection of parents and of breeding systems. Estimates of heritability of horticulturally important traits have been obtained in various fruit and nut crops, including sweet cherry (8), peach (11), walnut (9), strawberry (4, 7, 10, 16), and plum (12). In pears, however, genetic

Materials and Methods

The population. The present study is based upon the breeding records of the USDA pear breeding program at Beltsville, Maryland (5), and is restricted to those progenies planted in the years 1962 through 1966 (2). The crosses were made for the purpose of genetic improvement and are without experimental design. The parents were selected nonrandomly on the basis of their possession of some desirable trait. Although progenies planted each year constitute essentially unique sets of crosses, leading to confounding of genotypic and environmental effects on the expression of fire blight resistance, preliminary studies (1, 2) indicated that under the natural epiphytotic conditions in the orchard, the incidence (% of trees with symptoms) and severity (mean fire blight score) for each year's planting reached comparable and stable levels after 7 years. The data are, therefore, considered to give reasonable estimates of inherent and differential levels of fire blight resistance.

The population studied consisted of progeny from 256 crosses. Reciprocal and repeated crosses were pooled for analysis. (The few progenies of selfs were excluded.) A minimum progeny size (n=11) for estimation of a mean was established, using Stein's 2-stage procedure (19). Relatively large values of d (1.0) and α (0.20) were chosen in order to include as many progenies as possible in the analysis. The parental population included 30 cultivars and 52 advanced selections. Each parent

studies of fire blight resistance have been based principally upon analysis of segregation data. The objective of this study was to apply quantitative analysis of breeding records to 1) estimate heritability for fire blight resistance within a pear breeding population, and 2) to estimate relative average combining abilities of cultivars and selections used as parents.

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