# Genetic behavior analysis for phytochemical traits in coriander: Heterosis, inbreeding depression and genetic effects

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## Abstract

Increasing fruit yield, fatty acids and essential oils content in coriander are the main objectives. Reaching them need to understand the nature of gene action and quantifying the heterosis and inbreeding depression. Six genetically diverse parents, their 15 $F_1$ one-way hybrids and 15 $F_2$ populations were evaluated under different levels of water treatments. Beside the water treatment and genotype effects, the genetic effects of general (GCA) and specific (SCA) combining ability and their interactions with water treatment were significant for all traits. Water deficit stress decreased all traits in both $F_1$ and $F_2$ generations except for essential oil content which were significantly increased due to water deficit stress. Under water deficit stress, a non-additive gene action nature was predominant in $F_1$ generation while an additive gene action nature was more important in $F_2$ generation for all the traits except fruit yield under severe water deficit stress. There was a positive high heterosis for the traits examined in some hybrids. Also, in $F_2$ generation even after inbreeding depression, some promising populations displayed appropriate mean performance. These show that the parents used for crossing had rich gene pool for studied traits. Therefore, selection between the individuals of relevant $F_2$ populations could be led to develop high yielding hybrids or transgressed lines.

**Keywords:** Coriander, combining ability, $F_1$ and $F_2$ generations, gene action, inbreeding depression

# Introduction

Coriander (*Coriandrum sativum* L.) is a member of Apiaceae family which has known as medicinal and industrial plant. Food characteristics caused to cultivate and wide spread of coriander. It is used for different applications such as food, drugs, cosmetics and perfumery industry (Neffati and Marzouk, 2008). Coriander fruit contains both fatty acids and essential oils. A petroselinic acid is a main component of the fatty acid consisting 85% of the total fatty acids. In industry, petroselinic acid is broken-down into lauric, adipic and $C_6$ dicarboxylic acids which are used for synthesizing detergents and nylon polimer (Murphy et al., 1994; Murphy, 1996). The fatty oil composition of coriander fruit has previously been characterized (Ramadan and Morsel, 2002; Ramadan and Morsel, 2006; Msaada et al., 2009a; Sriti et al., 2009).

The essential oils in coriander have become interesting alternative for other natural components in food (Wong and Kitts, 2006; Donega et al., 2013). Also, the essential oils are used to flavor or remove unpleasant odors of some products in food industry (Matasyoh et al., 2009; Neffati and Marzouk, 2010). Essential oil composition of coriander fruit has previously been quantified (Msaada et al., 2007; Msaada et al., 2009b; Sriti et al., 2009, Neffati et al., 2011). Coriander essential oil includes 60-70% linalool has the pleasant characteristics odor (Lubbe and Verpoorte, 2011). Also, many medicinal properties have been attributed to coriander essential oil, including antibacterial (Burt, 2004; Lo Cantore et al., 2004), antioxidant (Wangensteen et al., 2004), antidiabetic (Gallagher et al., 2003) and anticancer (Chithra and Leelamma, 2000) and anti- antimicrobial activities (Matasyoh et al., 2009; Begnami et al., 2010; Neffati et al., 2011).

It was revealed that the amount and composition of substances and secondary metabolites affected by water deficit stress in some medicinal plants (Charles et al., 1990; Petropoulos et al., 2008). In some studies, an enhancing effect of water deficit stress on the biosynthesis of essential oils observed (Jaafar et al., 2012; Alinian et al., 2016). Under the stressful growth condition, secondary metabolites and/or substances production in plants enhanced for preventing an oxidization in the plant cells. Similarly, under water deficit stress an essential oil content may be increased. In case of fatty acids, there are evidences about the decreasing effect of water deficit stress on fatty acids content and yield (Hamrouni et al., 2001; Bettaieb et al., 2009; Bettaieb et al., 2011). To decrease adverse effects of drought stress on farmers' economy through lowering the yield of common crops, cultivation of medicinal plants with improved potential of secondary metabolites production under drought-affected areas could be suggested as an alternative approach (Alinian et al., 2016).

Consideration the statements, for increasing essential oil and fatty acids yield in coriander, reaching drought-tolerant cultivars with high fruit yield and fatty acids and essential oil content through plant breeding could be possible. Generally, plant breeding is known as a more stable approach and a complementary for decreasing the deleterious effects of water deficit stress through the development of genotypes which can grow and produce suitable essential oil yield under water deficit stressed environments. Any successful plant improving program depends on an understanding the nature of gene action involved in the inheritance of that traits under target growth condition. Griffing's (1956) diallel analysis has used to uncover the behavior of genes involved in controlling of the traits. This method has also used to estimate variance of GCA and SCA in different self-pollinated and open-pollinated crops (Khan et al., 2009; Blank et al., 2012; Townsend et al., 2013; El-Gabry et al., 2014; Khodadadi et al., 2016b; Khodadadi et al., 2017; Kaushik et al., 2018; Teodoro et al., 2019; Schegoscheski Gerhardt et al., 2019).

The heterosis phenomenon in $F_1$ hybrids can address the SCA and GCA of relevant parents. Therefore, heterotic breeding search for valuable hybrid combinations which have the commercialization potential. On the other hand, inbreeding depression measures the amount of vigor reduction in segregating generations due to self-pollination (Joseph and Santhoshkumar, 2000).

Diallel analysis on $F_1$ crosses has previously been done to estimate genetic parameters and combining ability in coriander (Khodadadi et al., 2016b). But, it is necessary to uncover the heterosis, inbreeding depression and repeatability of genetic estimates through $F_2$ diallel analysis to establish a successful breeding program for improving coriander fruit quantity and quality under water limiting conditions in coriander.  The objectives of this study were understanding gene action nature in controlling fruit yield and some phytochemical traits and identifying heterosis and inbreeding depression potential in coriander under different levels of water treatment.

## Materials and methods

### Plant material and growth conditions

Genotypes used for making diallel crosses had been evaluated in a preliminary experiment for drought tolerance by Khodadadi et al. (2016a). The characteristics of selected parental genotypes were summarized in Table 1. All the six parents contributed to produce 15 $F_1$ hybrids (without reciprocals) through half diallel mating system in 2015. A part of these $F_1$ hybrids' seed were used to produce 15 $F_2$ generations through self-pollination in the isolated condition. All of the six parents, 15 $F_1$ hybrids and 15 $F_2$ generations were evaluated under three levels of irrigation regimes. A field trial consisted three experiments close together 1 meter distance. These experiments were well watered (WW), moderate water deficit stress (MWDS) and severe water deficit stress (SWDS). Each of these experiments carried out through the randomized complete block design with three replications at the research field of Tarbiat Modares University (51° 09 ′E; 35° 44′ N; altitude 1265 m), Iran during the growing season of 2017. In WW experiment, a set of genotypes were well watered overall the experiment period. In MWDS experiment, a set of genotypes were well watered until an appearance of the stem when watering was withdrawn until the end of the flowering stage at which point one recovery watering applied. In SWDS experiment, watering was similar to WW experiment until an appearance of flowering stage and after which watering was cut off completely. The research field soil physical and chemical characteristic presented in Table 2.

## Trait Measurements

The phytochemical traits include essential oil content (EOC), fatty acid content (FAC), essential oil yield (EOY) and fatty acid yield (FAY), fruit yield per plant (FY) were measured. For measuring fruit yield of parents and relevant $F_1$ hybrids 10 plants were harvested from each of the experimental plots. In $F_2$ generations 30 plants were harvested from each of the experimental plots. For extracting the essential oil, 30 g of dried coriander fruits were well powdered and subjected to hydro-distillation in Clevenger-type apparatus for 120 min. Essential oil content (%w/w) was computed through the weight (g) of essential oil per 100 g of fruit (Khodadadi et al., 2016b). Also, essential oil yield was computed through multiplying the essential oil content by fruit yield per plant (g). For measuring fatty acid content, two grams of powdered fruit sample of coriander were subjected to Soxhlet apparatus with 250 ml of petroleum ether for 6 h. Fatty acids were removed after mixture filtration and solvent evaporation under reduced temperature and pressure (Alinian and Razmjoo, 2014; Khodadadi et al., 2016b). Finally, fatty acid yield was estimated by multiplying fatty acid content with fruit yield per plant (g) for each plot.

## Statistical analysis

The datasets were firstly tested for normality using the Anderson and Darling normality test. The analysis of variance for GCA and SCA effects were done according to Griffing's (1956) method 2, model 1 using a SAS program suggested by Zhang et al. (2005). Mean values of traits in water treatments were compared using the least significant difference (LSD) method at 5% level of probability. Estimates of $\sigma_g^2$ (general combining ability variance) and $\sigma_s^2$ (specific combining ability variance) were computed according to the random-effects model (Zhang et al., 2005). The GCA /SCA ratio was computed according to the method proposed by Baker (1978) (Equation 1).

$$\mathrm{GCA/SCA_{ratio}} = \frac{2\sigma_g^2}{2\sigma_g^2 + \sigma_s^2} \quad (1)$$

The best parent heterosis was calculated in $F_1$ hybrids using the formula suggested by Fonseca and Patterson (1968) (Equation 2).

$$\mathrm{Heterosis} = \frac{F_1 - BP}{BP} \quad (2)$$

where $F_1$ and BP are target hybrid and best parent values, respectively. Also, the observed inbreeding depression (ID) was estimated as a percent of the decrease in $F_2$ mean when compared with $F_1$ hybrid mean according to the formula suggested by Khan et al. (2009) (Equation 3). The $\overline{F_1}$ is the mean value of $F_1$ hybrid and $\overline{F_2}$ is the mean value of $F_2$ generations mean of parents.

$$\mathrm{ID}(\%) = \frac{\overline{F_2} - \overline{F_1}}{\overline{F_1}} \times 100 \quad (3)$$

All statistical analysis were done using Statistical Analysis System (SAS) (SAS Institute, 1992) and graphs generated using Excel Microsoft Office Software.

# Results and discussion

## Combined analysis of variance for traits under water treatments

The combined analysis of variance revealed the presence of a significant difference between water treatments for all of traits in both $F_1$ hybrids and $F_2$ generations (Table 3). There was a high significant difference between $F_1$ hybrids and also between $F_2$ generations for all of studied traits. These observations indicate that parent selection for diallel crosses had been properly done. Along with the main water treatment and genotype effects, the genotype × water treatment interaction effect was significant for all traits in both $F_1$ hybrids and $F_2$ generations (Table 3). Being significant genotype ($F_1$ hybrids + $F_2$ generations) × water treatment interaction refers to different growth response of genotypes in differently watered growth conditions.

Analysis of variance for genetic effects revealed that both additive and non-additive gene actions are involved in the expression of traits in both $F_1$ hybrids and $F_2$ generations. Also, significant GCA × environment and SCA × environment interactions effect for all traits in both $F_1$ and $F_2$ generations (Table 3) reveal that general combing ability of parents and specific combining ability of hybrids were differently determined by additive and non-additive gene actions under different water treatments, respectively. Therefore, selection for parent with high GCA or hybrid with high SCA should be done according to the condition of target cultivating environment.

## Effect of water deficit stress on measured traits

Generally, results indicated that fruit yield, essential oil yield, fatty oil content and fatty oil yield were negatively affected by water deficit stress in both $F_1$ hybrids and $F_2$ generations in coriander. But essential oil content was significantly increased under water deficit stress. (Table 4).

## Effect of water deficit stress on fruit yield

As shown in table 4, fruit yield was significantly affected by water treatments. The highest fruit yield obtained in well-watered condition while the minimum fruit yield obtained in severe water deficit stress in both $F_1$ hybrids and $F_2$ generations. A reduction in fruit yield of coriander under water deficit condition also reported by Nadjafi et al. (2009) and Khodadadi et al. (2016b). In other aromatic and medicinal crops, similar results observed by Zehtab-Salmasi et al. (2006) in dill (*Anethum graveolens* L.), Bannayan et al. (2008) in Plantago ovata and Nigella sativa, Laribi et al. (2009) in caraway (*Carum carvi* L.), Ekren et al. (2012) in purple basil (*Ocimum basilicum* L.) and Alinian and Razmjoo (2014) in cumin under drought stress condition. A fruit yield reduction under drought stress occurred through insufficient photosynthesis due to stomata closure and thereafter a reduction in $CO_2$ uptake (Rebey et al., 2012), shortening flowering and fruit setting periods and preferential allocation of assimilates to the roots rather than the shoots (Alinian and Razmjoo, 2014).

## Effect of water deficit stress on essential oil content and essential oil yield

The largest value of essential oil content obtained in the moderate water deficit stress while the lowest essential oil content recorded in well-watered for both $F_1$ hybrids and $F_2$ generations. Results indicate that drought stress has a positive effect on the essential oil content in coriander. Increasing in the essential oil content by progress in drought stress has also been documented by Baher et al. (2002) in *Satureja hortensis* L, Yassen et al. (2003) in *Ocimum basilicum* L., Omidbaigi et al. (2003) in sweet basil, Dunford and Vazquez (2005) in Mexican oregano, Khalid (2006) in *Ocimum basilicum* L. and *Ocimum americanum* L., Petropoulos et al. (2008) in parsley, Bettaiebet al. (2009) in *Salvia officinalis* L., Ekren et al. (2012) in *Ocimum basilicum* L. and Alinian et al. (2014) in cumin.

Whereas, drought stress leads to decrease in essential oil yield in both $F_1$ hybrids and $F_2$ generations (Table 4). So that the highest value of essential oil yield obtained in the well-watered condition and the lowest essential oil yield observed in severe water deficit stress for both $F_1$ hybrids and $F_2$ generations (Table 4). Similar results were reported by Singh and Ramesh (2000), Zehtab-salmasi et al. (2001), Farahani et al. (2009) and Alinian and Razmjoo (2014). Essential oil yield depends on essential oil content and fruit yield. Because drought stress had a more reducing effect on fruit yield rather than an increasing effect on essential oil content, therefore, essential oil yield reduced under water deficit stress conditions (Farahani et al., 2009).

## Effect of water deficit stress on fatty oil content and yield

The largest fatty oil content and yield values obtained in well-watered and the least fatty oil content and fatty oil yield values were obtained in severe water deficit stress for both $F_1$ hybrids and $F_2$ populations. Similarly, Singh and Ramesh (2000) in rosemary, Zehtab-Salmasi et al. (2006) in dill (*Anethum graveolens* L.), Hamrouni et al. (2001) in safflower, Bettaieb et al. (2009) in *Salvia officinalis* L. and Bettaieb et al. (2011) in cumin (*Cuminum cyminum* L.) observed that the significant decreasing effect of water deficit stress on fatty oil content and fatty oil yield.

## Nature of gene action

A significant GCA and SCA variances for all traits in both $F_1$ hybrids and $F_2$ populations indicate that both additive and non-additive gene actions are contributed to determine these traits. Khodadadi et al. (2016b) reported that both non-additive and additive gene actions for the inheritance of different traits are important in coriander.

GCA/SCA ratio reflects the degree of trait which transmitted to the progeny. When the GCA/SCA ratio are closer to unit and zero show that additive and non-additive gene actions are mostly involved in inheritance of the trait, respectively. Consideration the GCA/SCA ratio, non-additive gene action was predominant for fruit yield, essential oil yield and fatty oil yield traits in $F_1$ and $F_2$ generations under well-watered condition (Table 5). The same gene action in $F_1$ and $F_2$ may be because of coupling phase linkage (Ramachandram and Goud, 1981). In advanced generations, when a coupling linkage present, additive genetic variance decrease and when the repulsion linkage present, additive genetic variance increase Robinson et al. (1960). Therefore, to improve fruit yield, essential oil yield and fatty oil yield traits under well-watered condition, selection should be delayed to the later generations of segregation. For fatty oil content, non-additive gene action nature was predominant in $F_1$ hybrids, while in $F_2$ generations the additive genetic effects were more important under well-watered condition (Table 5). The inconsistency in $F_1$ and $F_2$ results is due to the breakdown of dominance effects and gen linkages. Also, essential oil content was predominantly governed by additive gene action in both $F_1$ hybrids and $F_2$ generations. Presence of mostly additive gene action in $F_2$ generation for fatty oil content and in both $F_1$ and $F_2$ generations for essential oil content suggests that selection programs can be effective in the $F_2$ and later generations for improvement of fatty oil content and essential oil content traits under well-watered conditions.

In severe water deficit stress, results of GCA/SCA ratio for fruit yield showed that non-additive type of gene action was predominant in both $F_1$ hybrids and $F_2$ populations (Table 5). Therefore, to improve fruit yield under severe water deficit stress condition, selection should be delayed to the later generations of segregation to loss of non-additive gene actions. For fruit yield under moderate water deficit stress and essential oil content, fatty oil content, essential oil yield and fatty oil yield under both moderate and severe water deficit stress conditions, the non-additive gene action in $F_1$ hybrids while an additive gene action in $F_2$ generation were more important (Table 5). Therefore, breeding programs based on selection can be effective in the $F_2$ and later generations for improvement of these traits under water deficit stress.

## Mean performance, heterosis and inbreeding depression

### Fruit yield

In well-watered condition, fruit yield varied from 2.40 ($P_6$) to 9.71 g ($P_2$) between the parents and ranged from 5.26 to 18.10 g ($H_{2}\times_{4}$) between the $F_1$ hybrids (Fig. 1A). Parental genotypes of the $H_{2}\times_{4}$ had approximately half yield (6.80–9.71 g) as compared to their hybrid. In $F_2$ generation, the fruit yield varied from 3.75 to 10.71 g between the hybrids (Fig. 1A). Similar to $F_1$ generation, in $F_2$ the highest fruit yield obtained by $H_{2}\times_{4}$. Also, in $F_1$ generations, almost all hybrids exhibited positive heterosis (7.82–115.40 %) in which $P_4$ involved hybrids mostly showed high heterosis (+80.91 to +89.74 %). Inbreeding depression from $F_1$ hybrids to $F_2$ generations ranged from −7.94 % to −42.80 % for fruit yield (Fig. 1A).

In moderate water deficit stress condition, fruit yield varied from 1.14 ($P_5$) to 5.27 g ($P_4$) between the parents and ranged from 1.17 to 10.03 g between the $F_1$ hybrids (Fig. 1B). A large fruit yield obtained in five $F_1$ hybrids including $H_{4}\times_{6}$ (10.03 g), $H_{1}\times_{4}$ (9.58 g), $H_{2}\times_{4}$ (8.93 g), $H_{4}\times_{5}$ (8.71 g) and $H_{3}\times_{4}$ (8.85 g). In $F_2$ generation, fruit yield varied from 1.08 to 9.29 g (Fig. 1B). $F_2$ generations relevant to the high yielding $F_1$ hybrids also exhibited the highest fruit yield. When $P_4$ and $P_6$ contributed as one of the mating partners, the large heterosis vigor obtained (+107.40 % to +159.59 %). Inbreeding depression from $F_1$ hybrids to $F_2$ populations had larger range for fruit yield (−0.36 % to −26.05 %) in moderate water deficit stress than well-watered (Fig. 1B).

In severe water deficit stress, fruit yield varied from 0.58 ($P_5$) to 2.24 g ($P_6$) between parents and from 0.22 to 4.77 g between $F_1$ hybrids (Fig. 1C). In $F_2$ generation, fruit yield varied from 0.21 to 4.28 g (Fig. 1C) and a large fruit yield obtained from $F_2$ populations derived from the $P_4$ and $P_6$ contributed hybrids. The heterosis values for fruit yield ranged between -64.68 and +154.54 % (Fig. 1C) and many of the hybrids exposed positive heterosis. Similar to moderate water deficit stress, inbreeding depression from $F_1$ hybrids to $F_2$ populations in severe water stress showed larger range (−0.59 to −22.66 %) than well-watered (Fig. 1C).

Higher heterosis and lower inbreeding depression in water deficit stressed conditions than those in well-watered condition reveal that the respective parents of hybrids probably were carriers of drought tolerance alleles could be homozygous recessive (Musembi et al., 2015). Therefore, their hybrids appeared superior in water deficit stressed conditions compared with the high yielding hybrids being superior in well water. In case of inbreeding depression from $F_1$ hybrids to $F_2$ generations, the heterozygote loci can maximally be 50 % breakdown. Therefore, an appearance of drought tolerance in $F_2$ generations could yet be kept by heterozygote genes.

## Essential oil content

In well-watered treatment, the essential oil content ranged from 0.140 % ($P_2$) to 0.550 % ($P_4$) between the parents and from 0.250 to 0.563 % between the $F_1$ hybrids (Fig. 2A). The highest essential oil content obtained in five hybrids of $P_4$ (0.440–0.563 %), followed by $H_1{\times}_3$ hybrid. In $F_2$ generation, essential oil content ranged from 0.237 to 0.545% (Fig. 2A) and five of the $F_2$ populations that a $P_4$ was one of mating partner exposed the highest essential oil content (0.431–0.545 %). In $F_1$ generation (Fig. 2A) many of hybrids showed positive heterosis (+2.42 to +62.20 %). Also, all the $F_2$ populations showed inbreeding depression (−2.07 to −9.06 %) (Fig. 2A).

In moderate water deficit stress, the essential oil content ranged from 0.257% ($P_5$) to 0.653 % ($P_4$) between the parents and from 0.343 to 0.997 % between the $F_1$ hybrids (Fig. 2B). The highest essential oil content recorded in five hybrids relevant to $P_4$ (0.667–0.997 %). In $F_2$ generation, essential oil content ranged from 0.258 to 0.907 % between the populations (Fig. 2B) and similar to the $F_1$ hybrids, five populations derived from $P_4$ showed the highest essential oil content (0.542-0.907 %). In $F_1$ generation all crosses exposed positive heterosis (+2.04 to +63.74 %) (Fig. 2B). Also, almost all the $F_2$ populations showed inbreeding depression (−9.00 to −36.52 %) (Fig. 2B).

In severe water deficit stress, the essential oil content ranged from 0.227 % ($P_5$) to 0.580 % ($P_4$) between the parents and from 0.320 to 0.770 % between the $F_1$ hybrids (Fig. 2C). The highest essential oil content obtained by five hybrids of $P_4$ (0.593–0.770 %). In $F_2$ generation, essential oil content was 0.191–0.560 % between the cross populations (Fig. 2C) and five derivatives of $P_4$ showed high essential oil content (0.499–0.560 %). In $F_1$ generation all hybrids showed positive heterosis (+2.30 to +74.12 %) and all of the $F_2$ populations showed inbreeding depression (−15.89 to −40.38 %) (Fig. 2C).

The ranges of heterosis and inbreeding depression were higher in water deficit stressed conditions compare to the well water condition. Generally, high heterosis along with high inbreeding depression refers the presence of genes with non-additive action and high heterosis along with the least inbreeding depression indicates the presence of genes with additive action (Shukla and Gautam, 1990). Low inbreeding depression in well water condition suggests that increased vigor of $F_1$s in such cases are expected to be mainly due to an accumulation of favorable additive action genes. Also, high inbreeding depression in water deficit stress condition indicates that non-additive action genes play major role in the inheritance of essential oil content.

Our results are in accordance with previous researches on inbreeding depression under water deficit stressed conditions (Cheptou et al., 2000; Armbruster and Reed, 2005). In $F_2$, even after inbreeding depression, some crosses exhibited good performance indicating the potential of these crosses to develop high essential oil content cultivars. The derivatives of the $P_4$ parent displayed better mean performance as compared to their parents even after segregation and inbreeding depression. Therefore, $P_4$ population could be used in the segregating generations to obtain genotypes with high essential oil content under different water treatments.

## Fatty oil content

In well-water, fatty oil content varied from 15.33 ($P_4$) to 22 % ($P_6$) between the parents and ranged from 16.33 to 26.67 % between the $F_1$ hybrids (Fig. 3A). The highest fatty oil content recorded for hybrids of $P_6$ ($H_1{\times}_6$ (26.67 %), $H_4{\times}_6$ (26.0 %), $H_3{\times}_6$ (25.0 %) and $H_2{\times}_6$ (23.0 %)) followed by $H_1{\times}_4$ hybrid. Parental genotypes of these promising hybrids also had nearly high fatty oil content (18.33–22.0 %). In $F_2$ generation, the fatty oil content varied from 14.94 to 22.54 % between the populations (Fig. 3A). The highest fatty oil content obtained in $F_2$ generation by $P_6$ hybrids and followed $H_1{\times}_4$, $H_2{\times}_5$, $H_1{\times}_2$ hybrids. In $F_1$ generation, heterosis ranged from +0.00 to +36.36 % for fatty oil content (Fig. 3A) and in $F_2$ generation, inbreeding depression for fatty oil content observed from −8.32 to −25.75 % (Fig. 3A).

In moderate water deficit stress, the fatty oil content varied from 11.67 ($P_2$) to 25.33 % ($P_6$) and 15.00 to 25.0 % between parents and $F_1$ hybrids, respectively (Fig. 3B). The highest fatty oil content observed in eight $F_1$ hybrids that $P_6$ involved in four crosses. In $F_2$ generation, fatty oil content varied from 14.68 to 25.98 % between hybrids (Fig. 3B) and the highest fatty oil content (22.89–25.98 %) recorded for three hybrids of $P_6$. The heterosis values for fatty oil content were

+1.96 to +33.33 % (Fig. 3B) and almost all hybrids showed positive heterosis. $F_2$ populations showed inbreeding depression for fatty oil content (−2.03 to −16.37 %) (Fig. 3B).

In severe water deficit stress, the fatty oil content varied from 10.33 ($P_2$) to 19.67 % ($P_6$) and 13.33 to 22.67 % between parents and $F_1$ hybrids, respectively (Fig. 3C). The highest fatty oil content were recorded in $F_1$ hybrids involving $P_6$ and followed by $H_1$×4 hybrid. In $F_2$ generation, fatty oil content varied from 12.85 to 20.41 % between the hybrids (Fig. 3C) and the highest fatty oil content was obtained from hybrids of $P_6$. The heterosis values for fatty oil content ranged from +4.26 to +30.77 % (Fig. 3C) and many of hybrids showed positive heterosis. The $F_2$ generations displayed inbreeding depression (−3.64 to −13.30 %) for fatty oil content (Fig. 3C). Overall, it was revealed that $P_6$ involved $F_2$ populations could be utilize for developing cultivars with high fatty oil content under different water treatments.

The ranges of heterosis and inbreeding depression were higher in well-watered than water stressed conditions. High heterosis is well-known to be a result of the effects of non-additive genes (Shalaby, 2013; Solieman et al., 2013; Singh et al., 2014). Therefore, the higher heterosis and inbreeding depression in well water condition suggest that non-additive gene actions were more predominant in well water condition compare to the water deficit stressed conditions. $F_2$ progenies derived from $P_6$ contributed hybrids showed better mean performance even after inbreeding depression than their parents indicating the presence of transgressive segregation for fatty oil content under different water treatments.

## Essential oil yield and fatty oil yield

In well-watered treatment, the essential oil yield ranged from 0.005 ($P_6$) to 0.037 g ($P_4$) among the parents and from 0.014 to 0.096 g between the $F_1$ hybrids (Fig. 4A). High essential oil yield was obtained for four $P_4$ crosses (0.057–0.096 g). In $F_2$ generation, essential oil yield ranged from 0.010–0.055 g between the cross generations (Fig. 4A) and four crosses of $P_4$ showed a high essential oil yield (0.033–0.055 g). In $F_1$ generation (Fig. 4A) almost all crosses indicated positive heterosis for essential oil yield (+7.48 to +213.91 %). Also, all of the $F_2$ populations showed inbreeding depression (−15.06 to −47.80 %) (Fig. 4A).

In moderate water stress, the essential oil yield ranged from 0.003 ($P_2$) to 0.034 g ($P_4$) between the parents and from 0.005 to 0.087 g between the $F_1$ hybrids (Fig. 4B). Highest essential oil yield was recorded for five $P_4$ crosses (0.058–0.087 g), followed by $H_1{\times}_6$, $H_3{\times}_6$, $H_5{\times}_6$ hybrids. In $F_2$ generation, essential oil yield ranged from 0.003–0.061 g between the cross population (Fig. 4B) and similar to the $F_1$ generation, crosses of $P_4$ showed highest essential oil yield (0.036–0. 0.061 g). In $F_1$ generation all crosses showed positive heterosis (+11.22 to +226.33 %) (Fig. 4B). Also, almost all of the $F_2$ populations showed inbreeding depression for essential oil yield (−6.88 to −44.40 %) (Fig. 4B).

In severe water stress, the essential oil yield ranged from 0.002 ($P_5$) to 0.010 g ($P_4$) between the parents and from 0.001 to 0.032 g between the $F_1$ hybrids (Fig. 4C). The highest essential oil yield was obtained in crosses of $P_4$ (0.021–0.032 g), followed by $H_1{\times}_6$, $H_3{\times}_6$, $H_5{\times}_6$ hybrids. In $F_2$ generation, essential oil yield ranged from 0.001–0.023 g between the cross generations (Fig. 4C) and progenies of $P_4$ and $P_6$ showed the highest essential oil yield. In $F_1$ generation, almost all crosses displayed positive heterosis (+26.01 to +208.31 %) (Fig. 4C). The $F_2$ generation showed inbreeding depression (−21.96 to −40.85 %) (Fig. 4C). Overall, results indicated that $P_4$ population could be used in the segregating generations to obtain genotypes with essential oil yield potential under different water treatments.

In well-water, the fatty oil yield varied from 1.12 to 3.41 g between parents and $F_1$ hybrids (Fig. 5A). The highest fatty oil yield was obtained from $H_2{\times}_4$, $H_1{\times}_4$ hybrids. In $F_2$ generation, fatty oil yield varied from 0.71 to 1.82 g between the generations (Fig. 5A) and highest fatty oil yield was noticed in generations derived from the hybrids of $P_4$. The heterosis values for fatty oil yield were ranged from -26.95 to +204.96 % (Fig. 5A) and all hybrids showed positive heterosis. $F_2$ populations displayed inbreeding depression for fatty oil yield (−21.88 to −49.31 %) (Fig. 5A).

In moderate water stress, the fatty oil yield ranged from 0.13 ($P_2$) to 0.85 g ($P_4$) between the parents and from 0.24 to 2.48 g between the $F_1$ hybrids (Fig. 5B). High values of fatty oil yield were recorded in hybrids involving $P_4$ and $P_6$. In $F_2$ generation, fatty oil yield ranged from 0.20–0.2.27 g between the cross generations (Fig. 5B) and the crosses of $P_4$ and $P_6$ showed high fatty oil yield. In $F_1$ generation (Fig. 5B) almost all of the hybrids showed positive heterosis (+3.42 to +191.18 %). Also, almost all of the $F_2$ population showed inbreeding depression (−4.14 to −31.64 %) (Fig. 5B).

In severe water stress, the fatty oil yield varied from 0.06 ($P_2$) to 0.45 g ($P_6$) and 0.04 to 1.04 g between parents and $F_1$ hybrids, respectively (Fig. 5C). High values of the fatty oil yield were recorded in $F_1$ hybrids involving $P_6$ and followed by hybrids of $P_4$. In $F_2$ generation, fatty oil yield varied from 0.03 to 0.89 g between the generations (Fig. 5C) and high values of the fatty oil yield was obtained from hybrids of $P_6$. The heterosis values of fatty oil yield ranged from +35.04 to +185.27 % (Fig. 5C) and many of the hybrids showed positive heterosis. The $F_2$ populations showed inbreeding depression (−4.53 to −27.02 %) (Fig. 5C). Overall, results indicated that $P_6$ and $P_4$ population could be used in the segregating generations to obtain genotypes with high fatty oil yield potential under different water treatments.

Inbreeding depression was higher in well water condition compare to water deficit stressed conditions for essential oil yield and fatty oil yield indicating that inbreeding depression was unstable across environments. Also, results revealed the higher heterosis values for essential oil yield and fatty oil yield than other traits indicating that non-additive genes were more responsible for the expression of these traits. These findings can be confirmed by the results of the GCA/SCA ratio in Table 5.

The utilization of hybrid vigor is one of the ways to improve yield in plant breeding. The existence of considerable degree of natural outcrossing had made these possible to use genetic diversity through production heterotic hybrids (Saxena *et al*., 1990). In coriander, heterosis cannot be exploited for higher production through commercial hybrids due to the nature of flower and poor seed recovery during hybridization. But estimation of heterosis for fruit yield, fatty oil and essential oils content will help in recognition crosses that can lead to isolate of advanced promising lines in segregating generation in coriander. Also, estimation of heterosis coupled with inbreeding depression shows that whether an amount of the vigor observed in segregating generations can be fixed in later generations by self-pollinating (Joseph and Santhoshkumar, 2000). The results showed that there was a positive heterosis for the traits examined in coriander which is an evidence for the existence of potential heterosis in Iranian coriander. In present study, the significant SCA effect indicates that there was non-additive gene effect, which could be the cause of the heterosis on the progenies observed and selection will not be effective in early generations. Hence, selection could be practiced in advance generations confirming to earlier reports.

The results showed that many of the $F_2$ population exposed inbreeding depression and it was higher for fruit yield, essential oil yield and fatty oil yield. Inbreeding depression mostly was higher in hybrids with high performing than hybrids with low and moderate performing. Soomro and Kalhoro (2000), Khan et al. (2007) and Khan et al. (2009) reported that $F_1$ hybrids with high performing were also correlated with higher inbreeding depression. Showing heterosis in $F_1$ and inbreeding depression in $F_2$ reveal the nature of gene action involved in the expression of the vigor in $F_1$ and depression in $F_2$. In $F_2$ generation, the offspring's of the parental genotypes $P_4$ and $P_6$ displayed better mean performance as compared to their parents and the selection in these crosses can provide transgressive gene recombinants for studied traits. $P_4$ and $P_6$ crosses are required to be subjected to the pedigree/progeny selection directly for reaching to the high potential cultivars. Also, $P_4$ and $P_6$ parents can be used as source of elite parents for synthetic cultivars (Khan et al., 2007; Khan et al., 2009) in coriander.

## Conclusion

Results indicated that water deficit stress negatively affected the fruit yield, essential oil yield, fatty oil content and fatty oil yield of coriander in both $F_1$ and $F_2$ generations. On the contrary, water deficit stress significantly increased the essential oil content of the coriander. Analysis of variance for genetic combining ability indicate that mean square due to GCA and SCA for all traits were highly significant in both $F_1$ and $F_2$ generations. Revealing the importance of additive and non-additive genetic nature in the expression of all traits in both $F_1$ and $F_2$ generations. Under water deficit stress conditions, non-additive gene action was predominant for studied traits in $F_1$, while additive gene effects were more important in $F_2$ generations except for fruit yield under severe water deficit stress. These results indicate that selection programs can be effective in the $F_2$ and later generations ($F_3$ or $F_4$) for improvement of the studied traits under water deficit stress conditions. Also, for improvement of fruit yield under severe water deficit stress, selection should be delayed to later generations ($F_3$ or $F_4$) of segregation for dissipation of non-additive gene action. There was a positive heterosis in coriander for all traits. In $F_2$, even after inbreeding depression, some promising generations displayed good performance and selection in such crosses can provide a better base for future. The progenies of the $P_4$ and $P_6$ parents displayed better mean performance as compared to their parents and the selection in these crosses provided transgressive gene recombinants for studied traits. It is also indicated that combined performance of $F_1$ hybrids and $F_2$ populations could be an appropriate criterion to recognizing the most promising populations to be used either as $F_2$ hybrids or as a resource population for further selection in advanced generations.

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**Table 1.** Coriander genotypes and their characteristics.

| Genotype | Parental code | Characteristics |
|---|---|---|
| Commercial | $P_1$ | Drought susceptible |
| TN-59-353 | $P_2$ | Relatively drought tolerant |
| TN-59-80 | $P_3$ | Drought susceptible |
| TN-59-160 | $P_4$ | Drought tolerant and relatively high yielding |
| TN-59-158 | $P_5$ | Highly drought susceptible |
| TN-59-230 | $P_6$ | Highly drought tolerant but low yielding |

**Table 2.** Soil properties of different layers of the experimental field.

| Soil depth (cm) | Sand (%) | Silt (%) | Clay (%) | Bulk density (g cm$^{-3}$) | FC (%) | Organic matter (%) | pH | EC (dS m$^{-1}$) |
|---|---|---|---|---|---|---|---|---|
| 0-20 | 70 | 15 | 15 | 1.2 | 16.5 | 1.61 | 7.75 | 1.3 |
| 20-40 | 68 | 18 | 14 | 1.4 | 19 | 1.45 | 7.75 | 1.28 |
| 40-60 | 66 | 18 | 16 | 1.48 | 15 | 1.09 | 7.74 | 1.26 |

FC, soil moisture at field capacity.

**Table 3.** Combined analysis of variance for phytochemical traits in the F$_1$ and F$_2$ generations under water treatments

| Source | df | Mean Squares | | | | | | | | | |
|---|---|---|---|---|---|---|---|---|---|---|---|
| | | FY | | EOC | | FOC | | EOY | | FOY | |
| | | F$_1$ | F$_2$ | F$_1$ | F$_2$ | F$_1$ | F$_2$ | F$_1$ | F$_2$ | F$_1$ | F$_2$ |
| Water treatment (WT) | 2 | 771.31$^{**}$ | 332.34$^{**}$ | 0.53$^{**}$ | 0.193$^{**}$ | 223.12$^{**}$ | 111.27$^{**}$ | 0.008$^{**}$ | 0.004$^{**}$ | 35.08$^{**}$ | 11.53$^{**}$ |
| Replication (WT) | 6 | 13.60 | 12.55 | 0.43 E$^{-3}$ | 0.33 E$^{-3}$ | 5.02 | 3.68 | 0.42 E$^{-3}$ | 0.26 E$^{-3}$ | 0.70 | 0.53 |
| Genotype (G) | 20 | 45.60$^{**}$ | 21.64$^{**}$ | 0.23$^{**}$ | 0.167$^{**}$ | 102.71$^{**}$ | 63.95$^{**}$ | 0.003$^{**}$ | 0.14 E$^{-2}$ | 2.25$^{**}$ | 0.93$^{**}$ |
| G × WT | 40 | 14.75$^{**}$ | 6.27$^{**}$ | 0.02$^{**}$ | 0.015$^{**}$ | 6.13$^{**}$ | 7.10$^{**}$ | 0.6 E$^{-3**}$ | 0.2 E$^{-3**}$ | 0.60$^{**}$ | 0.23$^{**}$ |
| GCA | 5 | 61.74$^{**}$ | 40.78$^{**}$ | 0.59$^{**}$ | 0.553$^{**}$ | 219.99$^{**}$ | 182.17$^{**}$ | 0.007$^{**}$ | 0.004$^{**}$ | 2.51$^{**}$ | 1.64$^{**}$ |
| SCA | 15 | 40.22$^{**}$ | 15.26$^{**}$ | 0.11$^{**}$ | 0.038$^{**}$ | 63.61$^{**}$ | 24.54$^{**}$ | 0.002$^{**}$ | 0.6 E$^{-3**}$ | 2.16$^{**}$ | 0.69$^{**}$ |
| GCA × WT | 10 | 35.18$^{**}$ | 19.27$^{**}$ | 0.02$^{**}$ | 0.022$^{**}$ | 8.65$^{**}$ | 13.54$^{**}$ | 0.001$^{**}$ | 0.6 E$^{-3**}$ | 1.13$^{**}$ | 0.69$^{**}$ |
| SCA × WT | 30 | 7.94$^{**}$ | 1.94$^{**}$ | 0.01$^{**}$ | 0.012$^{**}$ | 5.29$^{**}$ | 4.95$^{**}$ | 0.4 E$^{-3**}$ | 0.1 E$^{-3**}$ | 0.42$^{**}$ | 0.08$^{*}$ |
| Error | 120 | 1.12 | 1.10 | 0.54 E$^{-3}$ | 0.87 E$^{-3}$ | 1.98 | 2.09 | 3.87 E$^{-5}$ | 3.1 E$^{-5}$ | 0.05 | 0.05 |

$^{**}$ and $^{*}$ are significant at 1% and 5% levels of probability, respectively. Fruit yield (FY), essential oil content (EOC), essential oil yield (EOY), fatty oil content (FOC), fatty oil yield (FOY).

**Table 4.** The mean of traits under different irrigation treatments in F$_1$ and F$_2$ generations of coriander.

| Water treatment | FY | | EOC | | FOC | | EOY | | FOY | |
|---|---|---|---|---|---|---|---|---|---|---|
| | F$_1$ | F$_2$ | F$_1$ | F$_2$ | F$_1$ | F$_2$ | F$_1$ | F$_2$ | F$_1$ | F$_2$ |
| Well-watered | 9.19$^{a}$ | 6.74$^{a}$ | 0.351$^{c}$ | 0.337$^{c}$ | 20.59$^{a}$ | 18.35$^{a}$ | 0.035$^{a}$ | 0.023$^{a}$ | 1.88$^{a}$ | 1.22$^{a}$ |
| Moderate water Stressed | 4.51$^{b}$ | 3.94$^{b}$ | 0.530$^{a}$ | 0.446$^{a}$ | 18.60$^{b}$ | 17.76$^{b}$ | 0.029$^{b}$ | 0.021$^{a}$ | 0.87$^{b}$ | 0.73$^{b}$ |
| Severe water Stressed | 2.35$^{c}$ | 2.18$^{c}$ | 0.477$^{b}$ | 0.377$^{b}$ | 16.83$^{c}$ | 15.81$^{c}$ | 0.013$^{c}$ | 0.009$^{b}$ | 0.43$^{c}$ | 0.37$^{c}$ |

In each column the values with common letters do not differ significantly. Fruit yield (FY), essential oil content (EOC), essential oil yield (EOY), fatty oil content (FOC), fatty oil yield (FOY).

**Table 5.** Analysis of variance for combining ability, variance components and GCA/SCA ratio.

| Water treatment | Estimate | FY | | EOC | | FOC | | EOY | | FOY | |
|---|---|---|---|---|---|---|---|---|---|---|---|
| | | $F_1$ | $F_2$ | $F_1$ | $F_2$ | $F_1$ | $F_2$ | $F_1$ | $F_2$ | $F_1$ | $F_2$ |
| Well Watered | GCA | 31.82$^{**}$ | 13.86$^{**}$ | 0.131$^{**}$ | 0.128$^{**}$ | 59.34$^{**}$ | 30.62$^{**}$ | 0.002$^{**}$ | 0.001$^{**}$ | 16.25$^{**}$ | 8.30$^{**}$ |
| | SCA | 21.19$^{**}$ | 4.85$^{**}$ | 0.018$^{**}$ | 0.014$^{**}$ | 28.44$^{**}$ | 6.88$^{**}$ | 0.001$^{**}$ | 0.26 E$^{-3**}$ | 26.53$^{**}$ | 6.08$^{**}$ |
| | Error | 1.65 | 1.42 | 0.45 E$^{-3}$ | 0.41 E$^{-3}$ | 2.33 | 2.19 | 3.4 E$^{-5}$ | 2.24 E$^{-5}$ | 0.08 | 0.05 |
| | $\sigma_g^2$ | 2.21$^{ns}$ | 0.53$^{*}$ | 0.005$^{**}$ | 0.005$^{**}$ | 1.29$^{ns}$ | 0.99$^{**}$ | 4.5 E$^{-5ns}$ | 3.64 E$^{-5**}$ | 0.03$^{ns}$ | 0.004$^{ns}$ |
| | $\sigma_s^2$ | 18.21$^{**}$ | 1.83$^{**}$ | 0.006$^{**}$ | 0.004$^{**}$ | 8.70$^{**}$ | 1.56$^{**}$ | 0.4 E$^{-3**}$ | 7.96 E$^{-5**}$ | 0.64$^{**}$ | 0.08$^{**}$ |
| | GCA/SCA | 0.12 | 0.37 | 0.62 | 0.68 | 0.23 | 0.56 | 0.18 | 0.48 | 0.09 | 0.10 |
| Moderate Water Stress | GCA | 65.85$^{**}$ | 48.31$^{**}$ | 0.323$^{**}$ | 0.307$^{**}$ | 101.93$^{**}$ | 119.15$^{**}$ | 0.006$^{**}$ | 0.003$^{**}$ | 2.873$^{**}$ | 2.147$^{**}$ |
| | SCA | 16.30$^{**}$ | 8.64$^{**}$ | 0.074$^{**}$ | 0.041$^{**}$ | 23.03$^{**}$ | 16.00$^{**}$ | 0.001$^{**}$ | 5.3 E$^{-4**}$ | 0.791$^{**}$ | 0.448$^{**}$ |
| | Error | 0.90 | 1.14 | 0.001 | 0.001 | 1.68 | 1.70 | 5.3 E$^{-5}$ | 5.0 E$^{-5}$ | 0.049 | 0.071 |
| | $\sigma_g^2$ | 2.06$^{*}$ | 1.65$^{**}$ | 0.010$^{*}$ | 0.011$^{**}$ | 3.29$^{*}$ | 4.30$^{**}$ | 1.8 E$^{-4*}$ | 1.2 E$^{-4*}$ | 0.006$^{*}$ | 0.003$^{**}$ |
| | $\sigma_s^2$ | 5.13$^{**}$ | 2.50$^{**}$ | 0.025$^{**}$ | 0.013$^{**}$ | 7.12$^{**}$ | 4.77$^{**}$ | 4.6 E$^{-4**}$ | 1.6 E$^{-4**}$ | 0.009$^{**}$ | 0.003$^{**}$ |
| | GCA/SCA | 0.45 | 0.57 | 0.46 | 0.62 | 0.48 | 0.64 | 0.44 | 0.60 | 0.41 | 0.53 |
| Severe Water Stress | GCA | 13.62$^{**}$ | 11.30$^{**}$ | 0.177$^{**}$ | 0.161$^{**}$ | 76.03$^{**}$ | 59.48$^{**}$ | 6.4 E$^{-4**}$ | 3.9 E$^{-4**}$ | 0.68$^{**}$ | 0.48$^{**}$ |
| | SCA | 4.75$^{**}$ | 3.58$^{**}$ | 0.044$^{**}$ | 0.008$^{**}$ | 22.73$^{**}$ | 11.56$^{**}$ | 2.3 E$^{-4**}$ | 8.4 E$^{-5**}$ | 0.20$^{**}$ | 0.12$^{**}$ |
| | Error | 0.80 | 0.75 | 0.001 | 0.001 | 1.94 | 2.37 | 2.9 E$^{-5}$ | 2.1 E$^{-5}$ | 0.03 | 0.03 |
| | $\sigma_g^2$ | 0.37$^{*}$ | 0.32$^{*}$ | 0.006$^{*}$ | 0.006$^{**}$ | 2.22$^{*}$ | 2.00$^{**}$ | 1.7 E$^{-5*}$ | 1.3 E$^{-5**}$ | 0.02$^{*}$ | 0.02$^{**}$ |
| | $\sigma_s^2$ | 1.32$^{**}$ | 0.94$^{**}$ | 0.014$^{**}$ | 0.002$^{**}$ | 6.93$^{**}$ | 3.06$^{**}$ | 6.6 E$^{-5**}$ | 2.1 E$^{-5**}$ | 0.06$^{**}$ | 0.03$^{**}$ |
| | GCA/SCA | 0.36 | 0.40 | 0.44 | 0.86 | 0.39 | 0.57 | 0.35 | 0.55 | 0.41 | 0.57 |

$^{**}$ ,$^{*}$ and $^{ns}$ are significant at 1% and 5% level of probability and not significant, respectively. General combining ability (GCA), specific combining ability (SCA), fruit yield (FY), essential oil content (EOC), essential oil yield (EOY), fatty oil content (FOC), fatty oil yield (FOY).

## Figure captions:

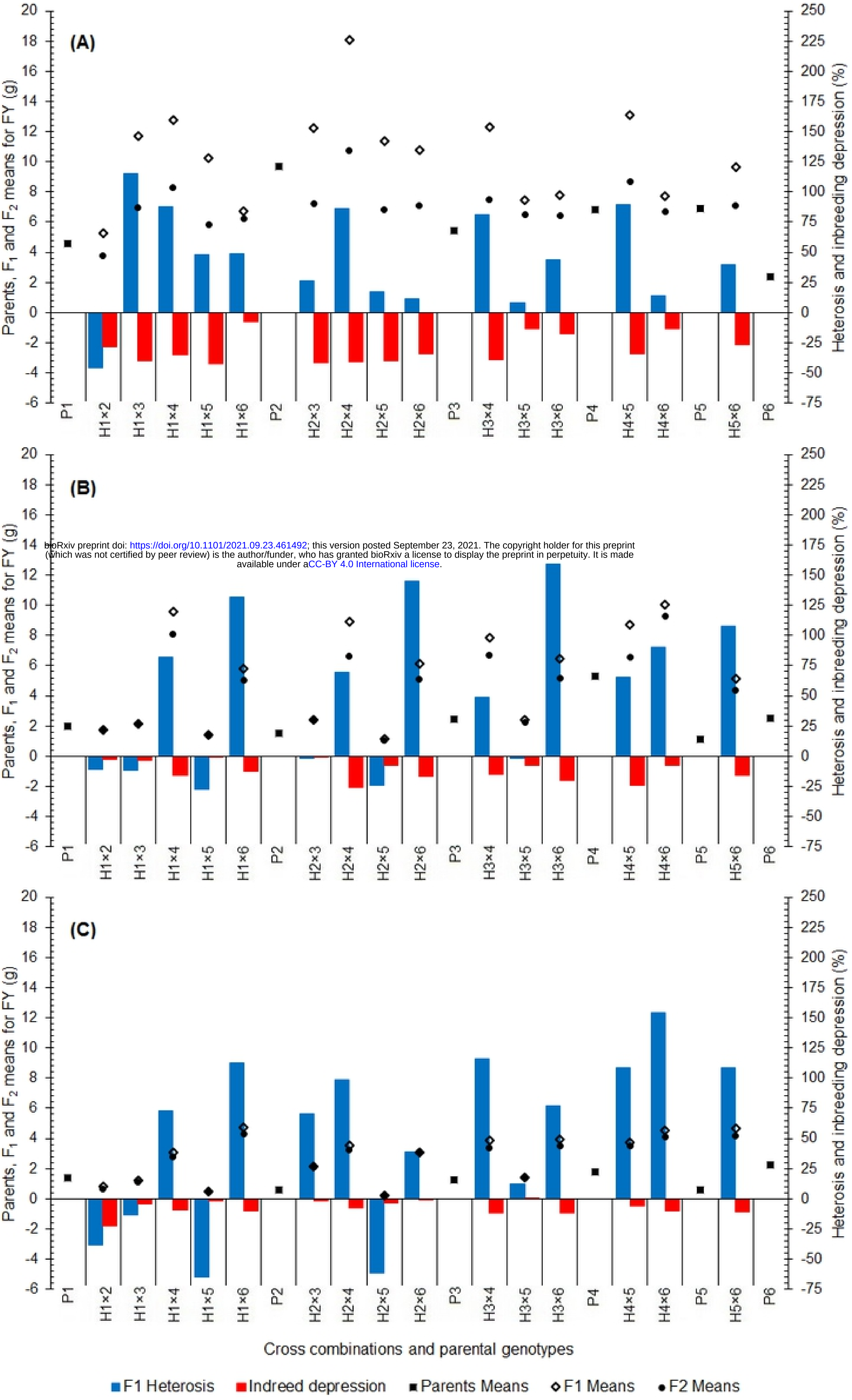
**Fig. 1.** Mean, heterosis and inbreeding depression for fruit yield in $F_1$ and $F_2$ generations of coriander crosses. **A:** Well Watered, **B:** Moderate Water Stress, **C:** Severe Water Stress

**Fig. 2.** Mean, heterosis and inbreeding depression for essential oil content in $F_1$ and $F_2$ generations of coriander crosses. **A:** Well Watered, **B:** Moderate Water Stress, **C:** Severe Water Stress

**Fig. 3.** Mean, heterosis and inbreeding depression for fatty oil content in $F_1$ and $F_2$ generations of coriander crosses. **A:** Well Watered, **B:** Moderate Water Stress, **C:** Severe Water Stress

**Fig. 4.** Mean, heterosis and inbreeding depression for essential oil yield in $F_1$ and $F_2$ generations of coriander crosses. **A:** Well Watered, **B:** Moderate Water Stress, **C:** Severe Water Stress

**Fig. 5.** Mean, heterosis and inbreeding depression for fatty oil yield in $F_1$ and $F_2$ generations of coriander crosses. **A:** Well Watered, **B:** Moderate Water Stress, **C:** Severe Water Stress



(A)
(B)
(C)
Parents, F1 and F2 means for FY (g)
Heterosis and inbreeding depression (%)
20
18
16
14
12
10
8
6
4
2
0
-2
-4
-6
250
225
200
175
150
125
100
75
50
25
0
-25
-50
-75
P1
H1×2
H1×3
H1×4
H1×5
H1×6
P2
H2×3
H2×4
H2×5
H2×6
P3
H3×4
H3×5
H3×6
P4
H4×5
H4×6
P5
H5×6
P6
Cross combinations and parental genotypes
F1 Heterosis
Indreed depression
Parents Means
F1 Means
F2 Means

Figure 1

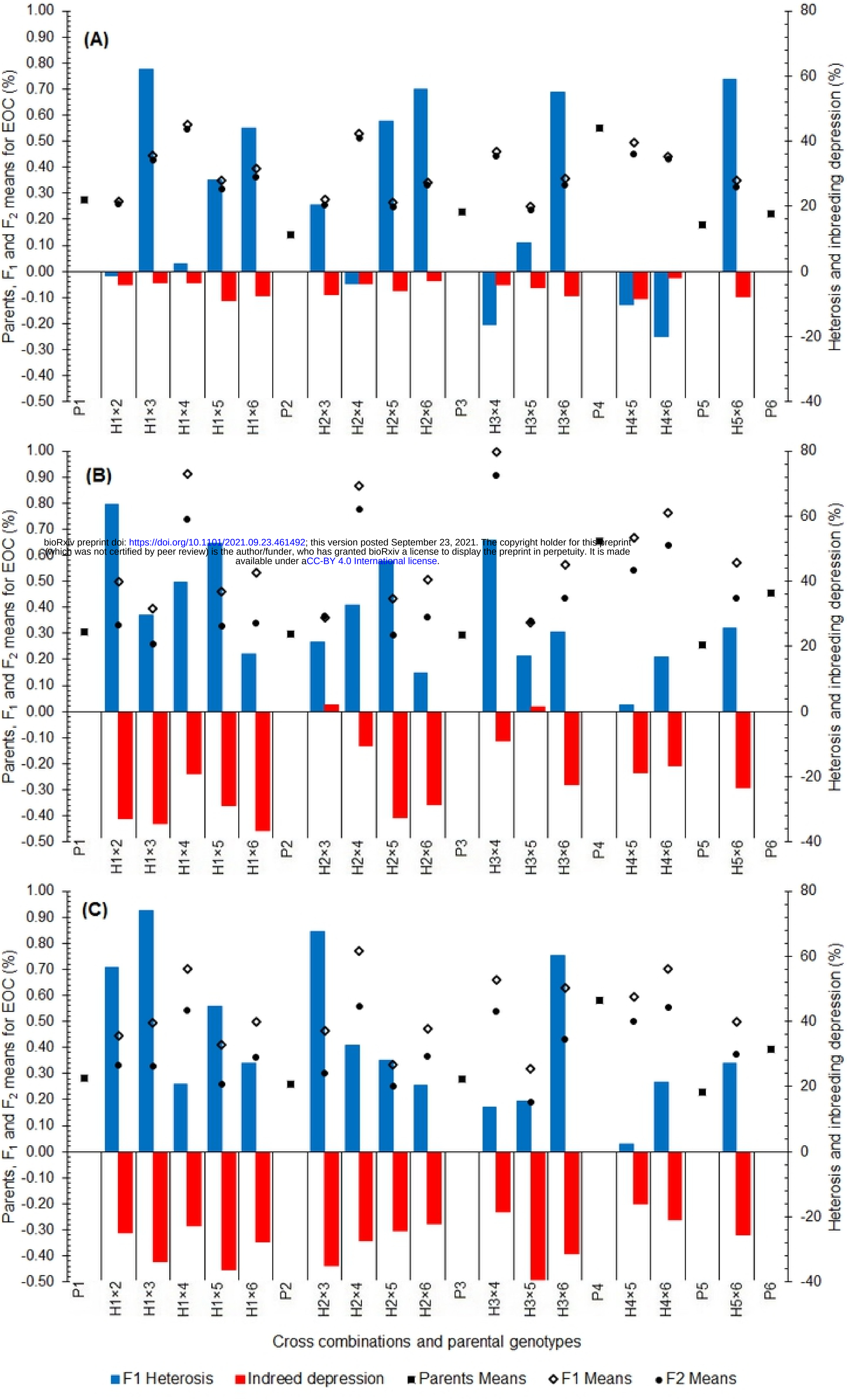

(A)
(B)
(C)
Parents, F1 and F2 means for EOC (%)
Heterosis and inbreeding depression (%)
1.00
0.90
0.80
0.70
0.60
0.50
0.40
0.30
0.20
0.10
0.00
-0.10
-0.20
-0.30
-0.40
-0.50
80
60
40
20
0
-20
-40
P1
H1×2
H1×3
H1×4
H1×5
H1×6
P2
H2×3
H2×4
H2×5
H2×6
P3
H3×4
H3×5
H3×6
P4
H4×5
H4×6
P5
H5×6
P6
Cross combinations and parental genotypes
F1 Heterosis
Indreed depression
Parents Means
F1 Means
F2 Means

Figure 2

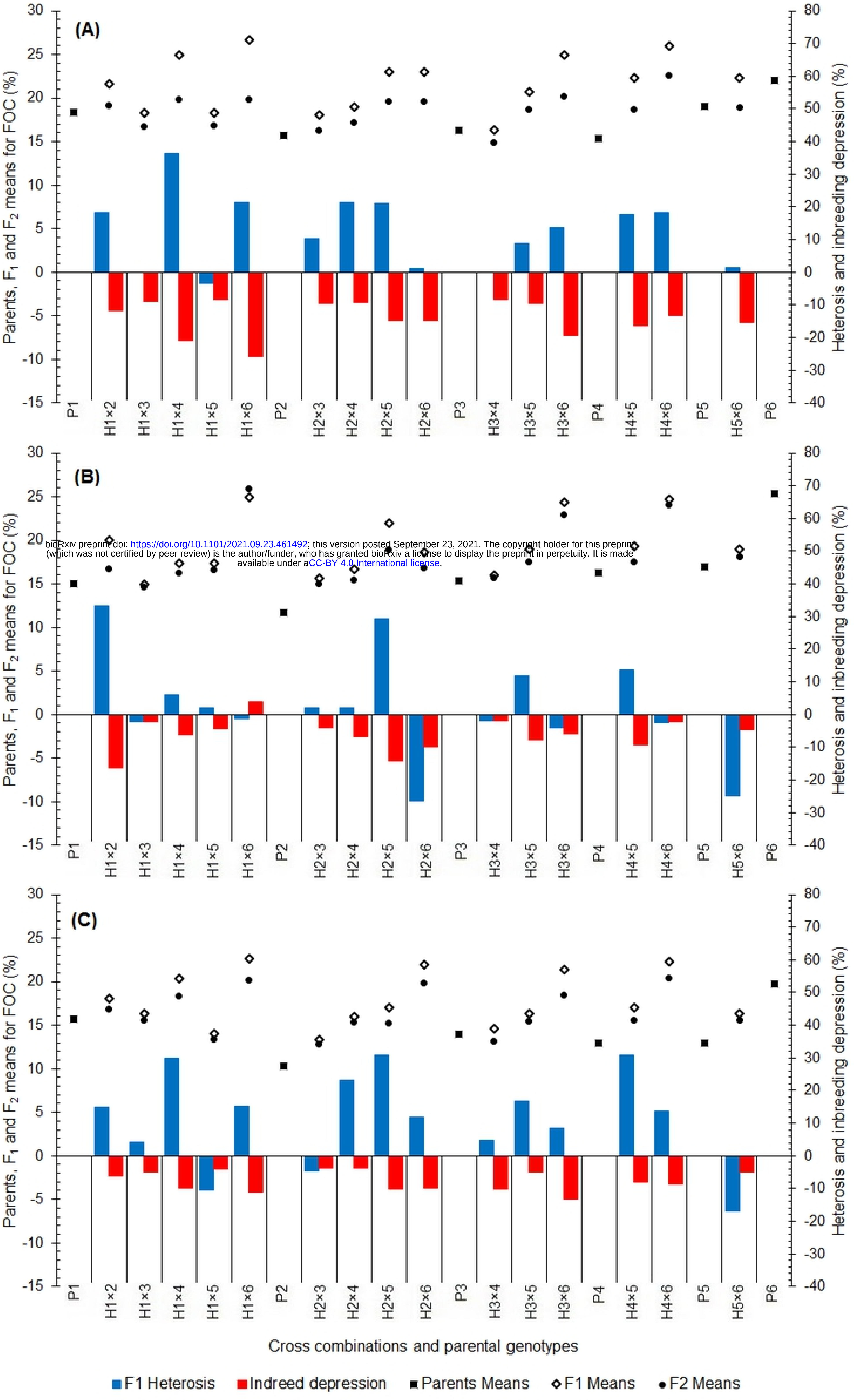

(A)
(B)
(C)
Parents, $F_1$ and $F_2$ means for FOC (%)
Heterosis and inbreeding depression (%)
30
25
20
15
10
5
0
-5
-10
-15
80
70
60
50
40
30
20
10
0
-10
-20
-30
-40
P1
H1×2
H1×3
H1×4
H1×5
H1×6
P2
H2×3
H2×4
H2×5
H2×6
P3
H3×4
H3×5
H3×6
P4
H4×5
H4×6
P5
H5×6
P6
Cross combinations and parental genotypes
F1 Heterosis
Indreed depression
Parents Means
F1 Means
F2 Means

Figure 3

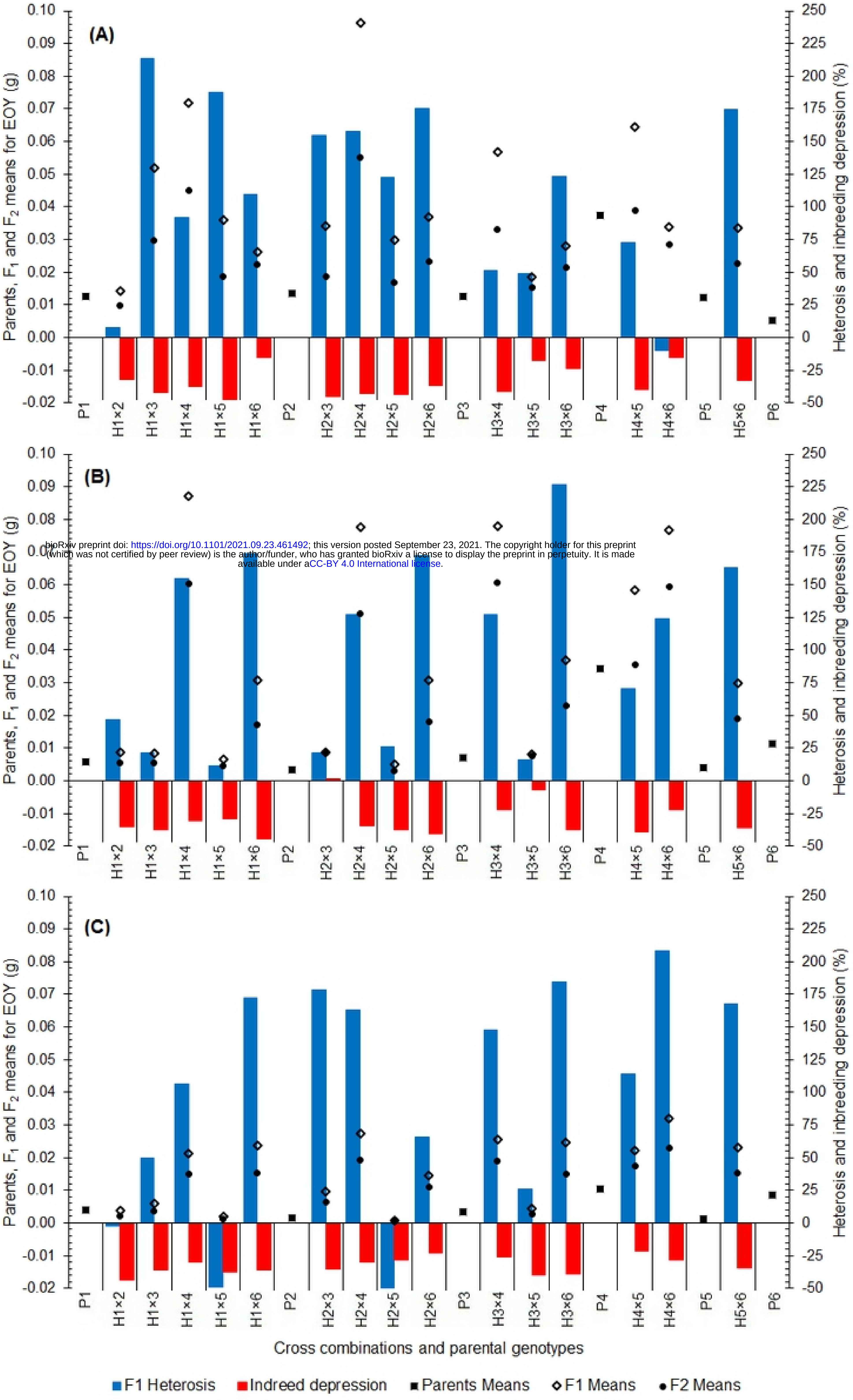

(A)
(B)
(C)
Parents, F1 and F2 means for EOY (g)
Heterosis and inbreeding depression (%)
0.10
0.09
0.08
0.07
0.06
0.05
0.04
0.03
0.02
0.01
0.00
-0.01
-0.02
250
225
200
175
150
125
100
75
50
25
0
-25
-50
P1
H1×2
H1×3
H1×4
H1×5
H1×6
P2
H2×3
H2×4
H2×5
H2×6
P3
H3×4
H3×5
H3×6
P4
H4×5
H4×6
P5
H5×6
P6
Cross combinations and parental genotypes
F1 Heterosis
Indreed depression
Parents Means
F1 Means
F2 Means

Figure 4

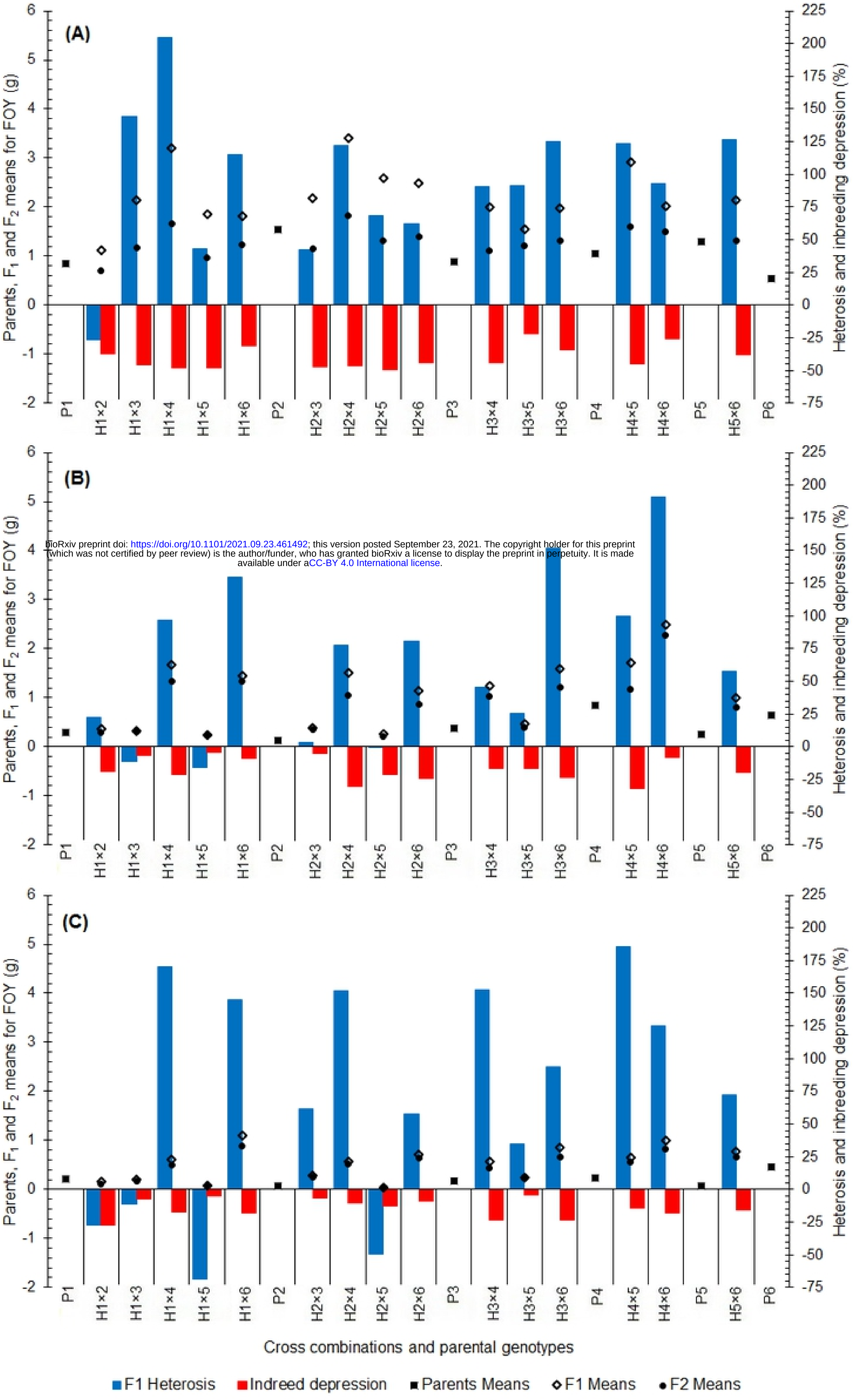

(A)
(B)
(C)
Parents, $F_1$ and $F_2$ means for FOY (g)
Heterosis and inbreeding depression (%)
6
5
4
3
2
1
0
-1
-2
225
200
175
150
125
100
75
50
25
0
-25
-50
-75
P1
H1×2
H1×3
H1×4
H1×5
H1×6
P2
H2×3
H2×4
H2×5
H2×6
P3
H3×4
H3×5
H3×6
P4
H4×5
H4×6
P5
H5×6
P6
Cross combinations and parental genotypes
F1 Heterosis
Indreed depression
Parents Means
F1 Means
F2 Means

Figure 5