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Eggplant fruit composition as affected by the cultivation environment and genetic constitution

Running title: Environment and genetic effects on eggplant composition

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ABSTRACT

BACKGROUND: No comprehensive reports exist on the combined effects of season, cultivation environment and genotype on eggplant (*Solanum melongena*) composition. We studied proximate composition, carbohydrates, total phenolics and vitamin C of eggplant fruits of three Spanish landraces, three commercial

hybrids and three hybrids between landraces cultivated across two environmental conditions (open field, OF; and, greenhouse, GH) for up to four seasons.
RESULTS: Season (S) had a larger effect than the genotype (G) for composition traits, except for total phenolics. GxS interaction was generally of low relative magnitude. Orthogonal decomposition of the season effect showed that differences within OF or GH environments were on many instances greater than those between OF and GH. Spanish landraces presented, on average, lower contents of total carbohydrates and starch and higher contents of total vitamin C, ascorbic acid, and total phenolics than commercial hybrids. Hybrids among landraces presented variable levels of heterosis for composition traits. Genotypes grown in the same season cluster together in the multivariate principal components analysis graph.
CONCLUSION: The cultivation environment has a major role in determining the composition of eggplant fruits. Environmental and genotypic differences can be exploited to obtain high quality eggplant fruits.

Keywords: fruit quality, genotype, hybrids, landraces, season, *Solanum melongena*

INTRODUCTION

Chemical composition of vegetables and fruits determines their nutritional value and organoleptic and bioactive properties. Although on occasion it is assumed that there are few intraspecific differences in the composition of vegetables and fruits, actually considerable diversity may exist.[1] Given the increasing demand of tasty and healthy vegetables by consumers[2] it is important to investigate the factors influencing composition of fruits and vegetables. In this respect, the cultivation environment and genotype are two major factors accounting for intraspecific differences in the edible parts of vegetables and fruits.[3-5] Therefore, understanding how environmental and genotypic factors and their interaction affect the composition of fruits and vegetables can contribute to improve their nutritional, organoleptic and bioactive properties.

Eggplant (*Solanum melongena* L.) is an important vegetable crop characterized by a low content in calories and relatively high contents in fiber and K, as well as high antioxidant activity, mostly resulting from a high content in phenolics.[6-9] There are several reports showing that considerable differences in composition exist among eggplant genotypes cultivated in a single season, or among seasons in a single cultivar.[7-13] However, despite the economic importance of the crop, few works have been performed in which the composition of a numberof eggplant varieties has been studied over several seasons.[14-16] These latter studies involved the determination of several chemical composition traits over two years in open field conditions in a variable number of accessions, which ranged from two in Raigón et al.[16] to 35 in Hanson et al.[14] The three works found differences in the composition among genotypes and years, but amazingly, in many of the composition traits studied, the year effect was larger than the genotype effect. For example, Hanson[14] using a wide diversity of eggplants found that the mean square for the year effect was greater than for the genotype effect for superoxide scavenging activity, total phenolics, and ascorbic acid. Also, Raigón et al.[16] found that differences among years were more important than the differences among the two varieties tested or the cultivation system (conventional vs. organic) in the composition profile, determined by dry matter, proteins, total phenolics, and mineral contents, of eggplant. Finally, Mennella et al.[15] found average yearly differences of up to three times in the content in solasonine, of 2.8-fold for delphinidin-3-rutinoside, and of almost twice for solamargine.

In subtropical and temperate climates, eggplant is commercially cultivated both in the open field (during the summer season) and in greenhouses (during the winter season).[17] Both cultivation environments present ample differences in temperature, relative humidity, photosynthetically active radiation, and CO_2 concentration, which affect the composition of many vegetables that are grown in both cultivation environments.[4] In eggplant, no comprehensive studies exist on the differences of fruit composition among fruits from open field and greenhouse cultivation. Only a single report by Khah et al.,[18] in which the effect of grafting was studied in greenhouse and open field environments, found that no significant differences existed between both environments for pH, soluble solids, acidity, and mineral composition of fruits of one commercial variety of eggplant. In tomato (*S. lycopersicum* L.), many more studies exist, and it is well known that fruits from open field plants present lower moisture and higher contents in sugars, ascorbic acid, carotenoids, and flavonoids than those cultivated in the greenhouse.[3,19,20] This generally results in a higher perceived quality from open field grown tomatoes when compared to greenhouse grown ones.[21]

Modern breeding in eggplant and other vegetables has led to the development of high yielding varieties adapted to greenhouse cultivation, which allows off-season production and higher economic returns.[22] There is evidence that in vegetables, selection for yield and long shelf life in modern breeding programmes has led to vegetable varieties that have reduced content of some nutrients due to a "dilution effect" indirectly caused by selection for higher yields.[23] In the case of eggplant modern varieties usually are F1 hybrids which are heterotic (i.e., higher values than the mean of the parents) for yield under the suboptimal conditions for fruit set in greenhouse cultivation.[24] In contrast, local landraces are normally highly homozygous[25] and adapted to open field cultivation.[24] In this respect, hybrids between local landraces situated at a high genetic distance have been proposed as an alternative to currently available commercial greenhouse-adapted F1 hybrids for open field cultivation.[22] Theferore, different varietal types, with a distinct genetic constitution and genetic background exist in eggplant, and this may affect composition, as occurred in tomato.[21] Raigón et al.[7] compared the dry matter content, protein, phenolics and mineral composition of eggplant fruits from commercial varieties, landraces, and hybrids between landraces for dry matter, proteins, phenolics, and minerals grown in greenhouse and found that landraces had, on average, higher contents of total phenolics, P, and Zn than commercial varieties. They also found that hybrids between landraces presented positive heterosis for dry matter and Na and negative heterosis for P, K, and Ca contents. However, this study was made for a single season. Regarding open field cultivation, no studies exist on the effect of the varietal type in eggplant fruit composition.

Here, we study the effects of the genotype, including different varietal types, and of the environment, including different cultivation environments (open field and greenhouse) and seasons within each environment in eggplant. The objective is to obtain information of relevance for understanding the factors which affect composition in the eggplant fruit.

EXPERIMENTAL

Plant material

Three eggplant landraces from Spain, three commercial F1 hybrids from different companies, and the three hybrids between the landraces were used (Table 1). The three landraces (Fig. 1) correspond to morphologically and genetically distinct cultivar types: long black (CS16), pickle-type (H11), and striped (IVIA371). The commercial F1 hybrids (Fig. 2) are representative of the most important cultivar types for greenhouse cultivation, i.e., the striped (Bandera) and black (Cristal and Ecavi) types. The hybrids between landraces (Fig. 1) were obtained by intercrossing the three landraces using a half diallel crossing scheme without reciprocals.

Growing seasons and cultivation conditions

Plants were cultivated across four growing seasons, which included two open field (OF) seasons (Open field 1 and 2; OF1 and OF2, respectively) and two greenhouse (using Venlo-type greenhouse) cultivation seasons (denominated Greenhouse 1 and 2; GH1 and GH2, respectively). The three landraces were grown across the four growing seasons, while commercial F1 hybrids and hybrids between landraces were cultivated across two growing seasons each: OF1 and GH1 for commercial F1 hybrids, and OF2 and GH2 for hybrids between landraces. Planting and harvesting dates of each of the growing seasons is indicated in Table 2. The two OF seasons present similar dates of planting and harvesting. However, the two GH seasons are quite different in the dates of planting and harvesting. GH1 and GH2 are, respectively early and late greenhouse cycles with harvesting dates in winter (January) for GH1 and late spring-early summer (June) for GH2.

The open field plot (GPS coordinates 39º28’55’’N, 0º20’11’’W) and greenhouse (GPS coordinates 39º29’01’’N, 0º20’27’’W) used for the experiments are situated in the campus of the Universitat Politècnica de València (Valencia, Spain). Ten plants per genotype were cultivated in each season. Plants were spaced 1 m between the rows and 0.4 m apart in the row in the open field and 1.7 m between the rows and 0.4 m apart in the row in the greenhouse. Plants were grown in soil in the open field conditions and in coconut fiber substrate in the greenhouse conditions and were drip irrigated.Fertilization was provided with the irrigation water. In the open field cultivation, plants were trained with horizontal strings in a hedge row system, while in the greenhouse they were pruned and trained with vertical strings. The standard cultivation techniques for eggplant were used in both OF and GH seasons.

Sample preparation

For each of the growing seasons, three samples of fruits of each genotype consisting of a minimum of 10 representative fruits per sample were used for the analyses. Fruits for the analyses were harvested (Table 2) when they reached the commercial maturity (as assessed by the fruit size and color and glossiness of the skin), and immediately sent to the Universidad Complutense de Madrid (UCM, Madrid, Spain) for analysis. Upon arrival to UCM, fruits were weighted (Table 1), and kept under refrigeration (4ºC) for no more than 24 h until processed. Then, they were peeled and cut in cubes, and one part of the cubes was homogenized, while the other was frozen and freeze-dried.

Composition traits analyzed

Proximate composition traits moisture, pH, and titratable acidity (TA) were measured in the fresh homogenate samples. Moisture ($g \cdot kg^{-1}$) was evaluated by desiccation to constant weight, pH with an electronic pH meter, TA (meq $NaOH \cdot kg^{-1}$) by titration with 0.1 NaOH to the phenolphthalein end point of pH 8.1. Proteins content ($g \cdot kg^{-1}$) were determined in freeze dried samples as N×6.25 after determination of N by the Kjeldahl method. Carbohydrates ($g \cdot kg^{-1}$) were determined in freeze-dried samples. Total available carbohydrates (TAC) were determined by the anthrone reaction colorimetric method, after hydrolysis with $HClO_4$; total soluble sugars (SS) were determined as the sum of the contents of glucose, fructose, sucrose, and maltose, obtained by HPLCdifferential refractive index detection; starch was determined as the difference between TAC and TSS; and, fiber content by the enzymatic-gravimetric method. Total vitamin C ($mg\cdot kg^{-1}$) was determined by HPLC-UV after extraction with metaphosphoric acid; ascorbic acid (AA) was quantified before and after reduction with L-cysteine, and dehydroascorbic acid as the differences between vitamin C and AA. Total phenolics (TP) were estimated using the Folin-Ciocalteu method and expressed as $mg\cdot kg^{-1}$. Full details of the procedures and equipment used for the determinations can be consulted elsewhere.[9]

Statistical analysis

Data of the three landraces, which had been evaluated for the four seasons, were subjected to a two-way analysis of variance (ANOVA) using a fixed-effects model to test the effects of the main factors genotype (G) and season (S) as well as their interaction (GxS). In order to obtain more information on the season effect, it was decomposed using orthogonal contrasts to test the significance of OF vs. GH, OF1 vs. OF2, and GH1 vs. GH2.[26] The total sum of squares was partitioned into the sums of squares for the genotype, season (and its components), interaction, and residual effects and expressed in percentage over the total sum of squares. Significance of differences among means for the traits measured was tested using the Student-Newman-Keuls multiple range test.

Additional ANOVA tests and orthogonal comparisons were performed in order to test the significance of the difference between eggplant landraces and commercial F1 hybrids grown across OF1 and GH1 seasons. Data from the eggplant landraces and their hybrids for OF2 and GH2 seasons were used to calculate the mid-parent heterosis (MPH, %) of the hybrids between landraces in each season by means of the formula

MPH=[(F1-MP)/MP]×100, where F1 is the hybrid value, and MP the mid parent value. Significance of mid-parent heterosis was determined using a t-test, based on the F1 and MP values and on the error mean square obtained from the ANOVA.[27] Principal components analysis (PCA) for the average data of all combinations of genotype and growing season was performed for standardized values of eggplant fruit composition traits using pairwise Euclidean distances among variety means.

RESULTS

Sums of squares for the genotype and season effects

An analysis of variance for the composition traits in the three landraces grown across the four seasons was performed. For all the composition traits measured, with the exception of TP, the percentage of the total sum of squares explained by the effect of season was greater than for the effect of genotype (Table 3). The season effect was significant for all the traits but one (maltose), and the sum of squares reached values of up to 89.3% for TA. In the case of the effect of genotype it was not significant for seven traits (proteins, pH, TSS, glucose, fructose, sucrose, and maltose), and the highest value for the contribution to the total sum of squares was that of TP (64.5%), followed at a large distance by DHAA (29.3%). The interaction between genotype and season (G×S) was significant for eight traits (moisture, TA, TAC, starch, total vitamin C, AA, and DHAA, total phenolics), but in all these cases had a much lower contribution to the total sum of squares than the effect of season (between 5.6 and 11.7 times lower for moisture and total vitamin C, respectively) (Table 3). The contribution of the residual effect to the total sums of square was generally low, with values below 30%, with the exception of proteins, sucrose, maltose, and fiber, which presented values above 40% (Table 3).

The orthogonal decomposition of the sums of squares of the season effect shows that there are significant differences between OF and GH cultivation environments for all traits except for TSS and its components (glucose, fructose, sucrose, and maltose) and fiber. This analysis also reveals that when comparing the two OF seasons and the two GH seasons there are also significant differences for the traits measured with few exceptions (maltose and fiber for the two OF seasons, and proteins, sucrose and maltose for the two GH seasons). For all the proximate and carbohydrate composition traits the contribution to the total sums of squares of the contrast between the OF and GH environments is smaller than the contribution of the contrast between the two OF seasons or the two GH seasons (Table 3). However, for total vitamin C and its components AA and DHAA, the contribution of the OF vs. GH environment is greater than between seasons of the same environment (Table 3). For several traits, the contribution to the total sums of squares of the difference among seasons within the same environment (i.e., between the two OF seasons, or between the two GH seasons) is ≥50%. This is the case of TSS, fructose and sucrose in the comparison between the two OF seasons, and of moisture, pH, TA, and starch in the comparison between the two GH seasons.

Genotype and season differences

The mean values for the proximate composition traits for the three landraces grown across the four seasons show that the three genotypes differed significantly each other for moisture content and TA (Table 4). For the moisture, IVIA 371 presented the highest mean value (93.6%), while H11 the lowest (92.7%); for TA, H11 presented significantly higher values than CS16 (1.51 and 1.40 meq NaOH·kg^{-1}, respectively). Significant differences among the type of environment (OF vs. GH) were found for the four proximate traits measured. The OF fruits, on average, had significantly lower moisture, protein content, and TA and higher pH than fruits from GH cultivation (Table 4). However, fruits of the GH1 season had significantly lower moisture content and TA than those of the OF2 season. The two OF seasons differed significantly for the four traits studied, with higher values for moisture and TA in OF2 and for proteins and pH in OF1. The two greenhouse seasons also differed significantly for all traits, except for proteins content, with higher values for moisture and TA in GH2 and for pH in GH1.

For carbohydrates content, H11 had higher TAC than CS16 and IVIA371, and higher starch and fiber contents than IVIA371 (Table 5). No significant differences were found among total and individual soluble sugars. In all genotypes, mean starch content (22.1 to 29.9 $g \cdot kg^{-1}$) was higher than TSS (17.7 to 21.2 $g \cdot kg^{-1}$), which in turn was higher than the fiber content (11.1 to 15.4 $g \cdot kg^{-1}$).Glucose and fructose were the individual sugars with higher concentrations, with values several times higher than those of sucrose and maltose, presented much lower levels (Table 5). The only significant differences observed between environment types was for TAC and its component starch, which on average were higher in GH (52.1 $g \cdot kg^{-1}$ for TAC and 31.6 $g \cdot kg^{-1}$ for starch) than in OF (38.9 $g \cdot kg^{-1}$ for TAC and 20.7 $g \cdot kg^{-1}$ for starch). However, significant differences among seasons were observed for all traits except maltose. The OF1 season presented lower values for TAC, TSS and its individual components glucose, fructose, sucrose, and maltose, as well as higher starch values than OF2 season. The GH1 season presented higher TAC and starch values but lower TSS, glucose, fructose, and fiber values than GH2 season. Amazingly, OF2 and GH2 seasons did not differ significantly for any of the carbohydrate traits studied.

Regarding the antioxidants, H11 was the genotype with higher average content of total vitamin C (196 $mg \cdot kg^{-1}$) as well as of AA (69 $mg \cdot kg^{-1}$), DHAA (127 $mg \cdot kg^{-1}$), and total phenolics (1109 mg·kg^{-1}), while IVIA371 presented the lowest values (103, 43, 60, and 638 mg·kg^{-1}, respectively), although for AA and total phenolics the difference with CS16 was non-significant (Table 6). The oxidized vitamin C form DHAA presented higher values than the reduced AA in all genotypes. The environment type had a significant effect for the four antioxidant traits measured, so that the highest levels for vitamin C, AA, and DHAA were found in the GH environment, while for total phenolics the OF environment presented higher values (Table 6). However, the AA content in OF2 was higher than in GH2 and the total phenolics was higher in GH1 than in OF2. Significant differences were found among the two OF seasons for the four antioxidants with highest values in OF2 for total vitamin C, AA, and DHAA contents, and in OF1 for total phenolics. Regarding the two GH environments, for the four antioxidant traits, the highest values were found in GH1.

Landraces vs. commercial F1 hybrids

The comparison of the three landraces and three commercial hybrids in OF1 and GH1 seasons shows that significant differences existed between the two genotype groups for the average values for several traits (Table 7). In both OF1 and GH1 seasons the landraces presented lower TAC and starch than the commercial F1 hybrids, and higher total vitamin C, AA, and total phenolics. Also, the landraces presented significantly higher moisture and TA than commercial F1 hybrids in the Open field 1. For the rest of traits no significant differences were found between the means of the two groups (Table 7). For all the traits in which significant differences between landraces and commercial F1 hybrids were detected, the range of variation of individual genotypes overlaped, with the exception of TA and total phenolics in OF1 in which the range of variation of local landraces did not overlap with that of commercial F1 hybrids. The largest relative difference between landraces and hybrids was for total phenolics in OF1, with average mean values for the landraces (1014 mg·kg^{-1}), 1.74-fold higher than for the commercial hybrids (582 mg·kg^{-1}) (Table 7).

Heterosis

Heterosis of hybrids among landraces was studied in seasons OF2 and GH2. No traits were found to present significant heterosis for all genotypes in both cycles (Table 8). For TAC and starch, positive significant positive heterosis was found in the three hybrids in the GH2 season. For proteins and vitamin C traits (total vitamin C, AA, and DHAA) in this same GH2 season, the three hybrids presented significant values for heterosis, although for each of the traits the values for heterosis of individual hybrids were contradictory (positive for the three traits in CS16×IVIA371, negative for the three traits in H11×IVIA371, and positive for total vitamin C and DHAA and negative for AA in CS16×H11) (Table 8). Significant negative heterosis was observed for moisture content in hybrids CS16×IVIA371 in both OF2 and GH2 seasons and for H11×IVIA371 in OF2. For the rest of traits no clear pattern was observed for heterosis, and the results depended on the specific combination of parents of the hybrids (Table 3). Remarkably, for TSS and the individual sugars, significant heterosis was only observed for CS16×IVIA371 in the OF1 season, with negative values for the heterosis for TSS and glucose and positive for starch (Table 8).

Multivariate analysis

The first and second components of the PCA accounted, respectively, for 42.1% and 24.4% of the total variation among combinations of genotype and season. The first component was positively correlated (component weights >0.15) with pH and starch, and negatively with moisture, TA, TSS and the four individual soluble sugars (glucose, fructose, sucrose, and maltose) (Fig. 3). The second component was positively correlated with moisture, and negatively with TAC and the three vitamin C traits (total vitamin C, AA, and DHAA).

The projection of the combinations of genotype and season in the PCA plot shows that genotypes cultivated in the same season cluster together (Fig. 4). In this respect, the four seasons plot in different areas of the graph and are clearly separated by the first component, with the exception of landrace H11 in OF2, which plots close to H11 grown in GH2 and to other accessions of this group. With the exception of genotype H11, genotypes cultivated in OF conditions present values of the first principal component above -2 and positive values of the second principal component. On the contrary, genotypes cultivated in the GH environments have values below -2 for the first component, negative values for the first component, or both. Genotypes cultivated in the OF1 season present positive values of the first and second components (i.e., associated to high pH and starch, and to low moisture, TSS and its constituent individual sugars, and low TAC and vitamin C and its components AA and DHAA), while those in the OF2 season present, in general, moderate negative values for the first component and positive ones for the second one. The genotypes cultivated in GH1 season present moderate values for the first component and high negative values for the second one (i.e., associated to low moisture, TA and TSS and individual sugars, and with high values for TAC and vitamin C), while those of GH2 are mostly characterized by high negative values for the first component (i.e., high moisture, TSS, and its components, and low pH and starch). Within each of the seasons, the three landrace genotypes are ranked in the same order in the second component, so that for this component IVIA371 has the highest values, CS16, intermediate, and H11 the lowest.

Also, according to this second component, the commercial F1 hybrids and the hybrids between landraces fall intermediate between the IVIA371 and H11 landraces (Fig. 4).

DISCUSSION

Differences in the composition of eggplants are known to affect its nutritional, organoleptic and bioactive properties.[8,9,12,13,28] Although a number of studies have been devoted to evaluate the diversity among collections of genotypes for the composition of eggplant,[7,8,11,12,14] few reports exist on the evaluation of the effect of the cultivation environment and season in the composition and their interaction with the genotype and varietal type. In fact, no studies are known to us in which the eggplant fruit composition is studied for more than two seasons, and only a few works address the composition of several eggplant genotypes in two open field seasons.[14-16] These works make more emphasis on the differences among genotypes,[14,15] or between conventional or organic cultivation[16] than in the combined effect of environment and genotype in the composition. Therefore, our work represents the first comprehensive study on the effects of environment, including different types of environment (open field and greenhouse), up to four seasons, and different categories of genotypes (landraces, commercial hybrids, and hybrids between landraces) in the composition of eggplant fruits.

The ranges of values observed for the composition traits studied are quite variable, but are in agreement with previous reports.[7,9,10,12,14,16] Our results confirm that the eggplant fruit has a high content of moisture, low content of sugars, relatively high fiber content, and high content in antioxidants, in particular of phenolics, which are present in the flesh at a concentration several times higher than that of vitamin C.[9,12,14] Taking into account that chlorogenic acid is the main phenolic constituent of the eggplant flesh,[11,15] and that the antioxidant activity of chlorogenic acid is similar to that of ascorbic acid,[29] it substantiates previous claims indicating that phenolics are the main responsible of the antioxidant activity of eggplant.[8,14] The results also confirmed that the predominant form of vitamin C in eggplant fruits is DHAA,[9] which may be of interest for physiology studies, as in most fruits and vegetables AA is the predominant vitamin C form.[30]

We have found that important differences exist in the composition of eggplant fruits depending on the genotype and, particularly, the season. This has important implications for obtaining fruits of high and stable quality. The evaluation of three landraces that are very different for the morphology, genetic background, and composition[16,31,32] over four seasons has shown that, although differences exist among genotypes for most traits, the differences among season are of major importance in the composition. This shows that, as occurs in other crops,[4,5] the environment plays a prominent role in determining the fruit composition of eggplant. In fact, for all traits, except total phenolics, the contribution of the season to the sums of squares of the ANOVA has been greater than that of the genotype, and the differences among seasons have been very large (more than four-fold) for some traits, like total soluble sugars, vitamin C, AA, and DHAA. In fact, the multivariate PCA analysis separates clearly the seasons in the PCA graph and all the genotypes grown in the same season are clustered together. Raigón et al.[16] also found that the season effect and the cultivation type (conventional vs. organic) was much larger than the genotype effect when comparing the composition of eggplants. Overall, these results reveal that the season effect has a larger effect than the genotype in the composition profile of the eggplant fruit.

Although the genotype x season (GxS) interaction has been significant for some traits, its contribution to the total sums of squares has been rather limited, indicating a low to moderate relative GxS interaction effect in eggplant. In this respect, for most traits the three landraces generally are ranked in the same order in the different seasons. The limited GxS interaction effect is also reflected in the fact that in the PCA analysis the three landraces follow the same ordination according to the second component, indicating that, independently of the season, their composition differences are consistent. Hanson et al.[14] also found that the ranking for antioxidant activity of 35 eggplant accessions grown over two years was consistent. Also, in different trials over several seasons *Almagro*-type pickling eggplants, like H11, generally present higher content in proteins, sugars, vitamin C, and total phenolics than the accessions for regular use, like CS16 and IVIA371.[9,12,16] This has important implications for eggplant breeding,[24] as it indicates that the eggplant materials identified as having superior composition in one season will likely maintain the superiority over the other materials in other seasons.

The open field and greenhouse growing conditions present many environmental differences,[4] and the physiological mechanisms that act in one environment may be different from those from the other,[33] and this may lead to differences in the fruit composition.[4,18,21,34] We have found considerable differences between open field and greenhouse grown eggplants in the eggplant fruit composition, but the differences among seasons within each type of environment (open field or greenhouse) have been larger, with the exception of vitamin C and its components AA and DHAA, than between open field and greenhouse environments. This shows that seasonal differences, either in the open field or greenhouse, may have a profound effect in the composition of eggplant fruits. It also indicates that eggplant fruits with a high quality composition may be obtained in both types of environments if the conditions are adequate. In contrast, in tomato, fruits from open field cultivation are generally of better quality than those from greenhouse cultivation.[3,21]

Local landraces and commercial hybrids of eggplant have a different genetic constitution, as landraces are pure lines highly homozygous, while commercial hybrids are F1 hybrids between pure lines with a moderate degree of heterozygosis.[35] Also, local landraces have evolved in open field conditions during the warm season, while commercial hybrids have been selected for off-season adaptation to greenhouse conditions.[24] Despite the divergent genetic constitution, the differences in composition between both types of materials have not been significant for most traits. The most relevant differences between both varietal types that have shown consistency in both open field and greenhouse conditions have been a higher starch content in commercial hybrids, which has resulted in a higher content in total carbohydrates, and lower content in ascorbic acid, leading to a lower total vitamin C, and total phenolics in commercial hybrids. The fact that compared to local landraces modern eggplant commercial hybrids present a higher starch content but similar levels of soluble sugars, indicates that the commercial hybrids have a similar sweetness, but a higher content in calories, than landraces. Several studies have shown that modern eggplant varieties have a generally lower content in phenolics than modern varieties.[11,12,16,36] Prohens et al.[12] hypothesized that indirect selection for low browning had resulted in a lower content in phenolics in modern varieties, and our work seems to be in agreement with this hypothesis, revealing that modern eggplant cultivars may have, on average, reduced bioactive properties compared to landraces. However, at present breeding programmes are underway to develop modern varieties with enhanced content in phenolics and low browning based on selection for low polyphenol oxidase activity.[37]

Hybrids between landraces have been proposed as an alternative to commercial F1 hybrids for open field production, as selected hybrids in which the parents are situated at a high genetic distance are heterotic for yield under these conditions.[17,22] When comparing hybrids between landraces with their parents for composition traits, Prohens et al.[12] and Rodríguez-Burruezo et al.[22] using open field cultivation conditions found that for soluble solids content, ascorbic acid and total phenolics contents, on average the hybrids between landraces were intermediate between both parents, although in some hybrids, positive or negative significant heterosis was found for one or more traits. On the other hand, Raigón et al.[7] when comparing both types of materials in greenhouse conditions found, on average, significant positive heterosis for dry matter, but not for protein or phenolics. However, these same authors also found a wide range of heterosisvalues for each of the traits among the hybrids between landraces. In our case, we have also found that the heterosis (positive or negative) depends on the particular hybrid under consideration and also on the cultivation environment, and no clear pattern of heterosis associated to the hybrid nature has been found for any of the traits studied. In fact, on many occasions in which significant heterosis is found for a trait in a specific hybrid in one environment and in the other environment the heterosis is non-significant or significant but of a different nature. Therefore, evidence of this work and from others[7,12,22] indicates general predictions of the heterosis for specific composition traits in hybrids between eggplant landraces are unreliable.

In summary, we have found that the environment plays a major role in determining the composition of eggplant fruits, and that large differences in composition may exist among seasons, even with the same cultivation system (open field or greenhouse). Considerable differences exist among individual genotypes in composition, which can be exploited for selection and breeding. Although for most traits no significant differences have been found among the different varietal groups (landraces, commercial hybrids, hybrids between landraces), landraces on average have a lower content in starch and higher content in antioxidants than commercial hybrids. Also, heterosis levels in hybrids between landraces for composition traits are highly variable and depends on the specific combination of parentals. This information will be useful to understand variability in the composition of eggplant fruits and in determining growing conditions and selecting plant material for obtaining eggplant fruits with improved nutritional, organoleptic, and bioactive properties.

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Table 1. Genotypes used for each of the three varietal types tested (landraces, commercial F1 hybrids, and hybrids between landraces), code used in the figures, origin, and fruit weight (mean±standard deviation) in the four seasons tested.

Genotypes	Origin	Fruit weight (g)			
		Open field 1 (OF1)	Greenhouse 1 (GH1)	Open field 2 (OF2)	Greenhouse 2 (GH2)
Landraces					
CS16	Barcelona, Spain	188±63	226±50	235±40	277±59
H11	Almagro, Spain	192±49	150±44	229±92	117±17
IVIA371	Valencia, Spain	371±41	244±60	321±17	263±113
Commercial F1 hybrids					
Bandera	Seminis Vegetable Seeds	319±65	251±89	---	---
Cristal	Semillas Fitó	302±51	309±39	---	---
Ecavi	Rijk Zwaan	292±47	342±33	---	---
Hybrids between landraces					
CS16×H11	Hybrid between CS16 and H11	---	---	262±38	266±85
CS16×IVIA371	Hybrid between CS16 and IVIA371	---	---	246±74	287±48
H11×IVIA371	Hybrid between H11 and IVIA371	---	---	225±68	329±37

Table 2. Dates for the planting and harvesting of the fruits used for the composition analyses for each of the four eggplant growing seasons used.

Growing season	Planting	Harvesting
Open field 1 (OF1)	May 2006	September 2006
Greenhouse 1 (GH1)	August 2006	January 2007
Open field 2 (OF2)	May 2007	September 2007
Greenhouse 2 (GH2)	February 2008	June 2008

Table 3. Percentage of the total sums of squares and significance of the effects of cultivar, environment (and the decomposition in its orthogonal components: Open field (OF) vs. Greenhouse (GH), Open field season 1 (OF1) vs. Open field season 2 (OF2), and Greenhouse season 1 (GH1) vs. Greenhouse season 2 (GH2)), the cultivar x environment interaction, and residual in three eggplant landraces cultivated in four environments(two seasons in OF and two seasons in GH).

	Genotype	Season (S)					
Traits[a]	(G)	Total	OF vs. GH	OF1 vs. OF2	GH1 vs. GH2	G×S Interaction	Residual
Proximate traits							
Moisture	17.7***	66.3***	1.3*	13.9***	51.1***	11.8***	4.2
Proteins	14.2ns	27.6*	11.7*	15.5*	0.3ns	6.8ns	51.4
pH	0.4ns	85.2***	23.3***	8.9***	53.1***	2.5ns	11.9
Titratable acidity (TA)	1.1**	89.3***	2.0***	34.1***	53.2***	8.0***	1.6
Carbohydrates							
Total available carbohydrates (TAC)	10.2***	75.1***	25.4***	17.2***	32.5***	8.6***	6.1
Total soluble sugars (TSS)	1.9ns	85.0***	1.2ns	61.5***	22.3***	2.8ns	10.3
Glucose	0.1ns	81.1***	0.3ns	65.8***	15.0***	2.7ns	16.2
Fructose	0.7ns	69.8***	2.4ns	50.0***	17.4***	3.2ns	26.3
Sucrose	6.0ns	19.0*	1.2ns	12.2*	5.6ns	25.7ns	49.4
Maltose	10.8ns	22.2ns	11.1ns	5.5ns	5.5ns	3.9ns	63.2
Starch	4.2**	79.7***	12.3***	3.3**	64.1***	9.6***	6.4
Fiber	27.8**	21.9**	0.1ns	2.4ns	19.4**	6.8ns	43.6
Antioxidants							
Total vitamin C	24.7***	68.8***	36.7***	19.5***	12.6***	5.9***	0.7
Ascorbic acid (AA)	16.3***	75.1***	30.0***	16.5***	28.6***	7.3***	1.3
Dehydroascorbic acid (DHAA)	29.3***	59.8***	36.0***	18.7***	5.2***	9.1***	1.8
Total phenolics	64.5***	27.6***	7.3***	12.6***	7.8***	4.7***	3.3

[a] ns, *, **, ***, indicate non-significant (P≥0.05), and significant at P<0.05, P<0.01, and p<0.001, respectively.

Table 4. Mean values for the proximate composition traits of eggplant fruits for the different levels of genotype, environment type, and season based on the three eggplant landrace genotypes tested for four seasons.

Factor	Moisture ($g \cdot kg^{-1}$)	Proteins ($g \cdot kg^{-1}$)	pH	Titratable acidity (meq $NaOH \cdot kg^{-1}$)
Genotype[a]				
CS16	933 b	7.2	5.32	14.0 a
H11	927 a	8.5	5.31	15.1 b
IVIA371	936 c	7.6	5.27	14.4 ab
Environment type[a]				
Open field (OF)	931 a	7.3 a	5.46 b	13.9 a
Greenhouse (GH)	933 b	8.3 b	5.14 a	15.1 b
Season[a]				
Open field 1 (OF1)	926 a	8.1 b	5.60 c	10.5 a
Open field 2 (OF2)	936 b	6.5 a	5.32 b	17.3 b
Greenhouse 1 (GH1)	924 a	8.4 b	5.43 b	10.8 a
Greenhouse 2 (GH2)	942 c	8.1 b	4.80 a	19.3 c

[a]Means separated by different letters within each of the levels genotype, environment type, and season, are significantly different at $P<0.05$, according to the Student-Newman-Keuls test.

Table 5.Mean values for the carbohydrate composition traits of eggplant fruits for the different levels of genotype, environment type, and season based on the three eggplant landrace genotypes tested for four seasons.

Factor	Total available carbohydrates (TAC; g·kg^{-1})	Total soluble sugars (TSS; g·kg^{-1})	Glucose (g·kg^{-1})	Fructose (g·kg^{-1})	Sucrose (g·kg^{-1})	Maltose (g·kg^{-1})	Starch (g·kg^{-1})	Fiber (g·kg^{-1})
Genotype[a]								
CS16	44.1 a	17.7	9.3	7.6	2.0	0.6	26.4 ab	13.4 ab
H11	51.1 b	21.2	9.3	8.5	1.9	1.3	29.9 b	15.0 b
IVIA371	41.2 a	19.1	9.0	8.2	1.1	1.0	22.1 a	11.1 a
Environment type[a]								
Open field (OF)	38.9 a	18.2	9.5	7.4	1.5	0.7	20.7 a	13.2
Greenhouse (GH)	52.1 b	20.5	8.9	8.8	1.8	1.3	31.6 b	13.4
Season[a]								
Open field 1 (OF1)	31.2 a	6.5 a	2.5 a	3.1 a	0.6 a	0.4	24.7 b	12.5 ab
Open field 2 (OF2)	46.5 b	29.9 c	16.5 b	11.7 c	2.3 ab	1.0	16.7 a	13.9 b
Greenhouse 1 (GH1)	62.6 c	13.4 b	5.5 a	6.2 b	1.3 ab	1.0	49.2 c	11.3 a
Greenhouse 2 (GH2)	41.5 b	27.5 c	12.2 b	11.3 c	2.4 b	1.6	14.0 a	15.4 b

[a]Means separated by different letters within each of the levels genotype, environment type, and season, are significantly different at $P<0.05$, according to the Student-Newman-Keuls test.

Table 6. Mean values for the antioxidant composition traits of eggplant fruits for the different levels of genotype, environment type, and season based on the three eggplant landrace genotypes tested for four seasons.

Factor	Vitamin C ($mg{\cdot}kg^{-1}$)	Ascorbic acid (AA; $mg{\cdot}kg^{-1}$)	Dehydroascorbic acid (DHAA; $mg{\cdot}kg^{-1}$)	Total phenolics ($mg{\cdot}kg^{-1}$)
Genotype[a]				
CS16	145 b	46 a	99 b	685 a
H11	196 c	69 b	127 c	1109 b
IVIA371	103 a	43 a	60 a	638 a
Environment type[a]				
Open field (OF)	102 a	37 a	65 a	882 b
Greenhouse (GH)	194 b	69 b	126 b	740 a
Season[a]				
Open field 1 (OF1)	54 a	20 a	34 a	1014 d
Open field 2 (OF2)	149 b	54 c	96 b	750 b
Greenhouse 1 (GH1)	233 c	91 d	142 c	843 c
Greenhouse 2 (GH2)	156 b	47 b	109 b	636 a

[a]Means separated by different letters within each of the levels genotype, environment type, and season, are significantly different at $P<0.05$, according to the Student-Newman-Keuls test.

Table 7.Average values and range for the fruit composition traits measured in two environments (Open field 1 and Greenhouse 1 seasons) of three eggplant traditional landraces and three modern F1 hybrid cultivars and probability of the orthogonal comparison between the average values of landraces and F1 hybrid cultivars.

Traits	Open field 1 (OF1)				Greenhouse 1 (GH1)			
	Landraces (L)		Hybrid Cultivars (H)		Landraces (L)		Hybrid Cultivars (H)	
	Mean	Range	Mean	Range	Mean	Range	Mean[a]	Range
Proximate traits								
Moisture ($g \cdot kg^{-1}$)	926	922-929	918^{***}	908-923	924	921-926	923^{ns}	919-925
Proteins ($g \cdot kg^{-1}$)	8.1	7.4-8.5	8.9^{ns}	8.5-9.5	8.4	7.9-9.0	7.3^{ns}	6.9-7.8
pH	5.60	5.52-5.69	5.56^{ns}	5.53-5.57	5.48	5.46-5.50	5.42^{ns}	5.35-5.50
Titratable acidity (TA; meq $NaOH \cdot kg^{-1}$)	10.5	9.7-11.2	8.5^{***}	8.2-8.8	10.8	9.9-11.5	11.3^{ns}	10.0-12.6
Carbohydrates								
Total available carbohydrates (TAC; $g \cdot kg^{-1}$)	31.2	20.5-39.8	37.8^{**}	36.2-39.3	62.6	55.1-66.4	72.6^{**}	65.2-82.9
Total soluble sugars (TSS; $g \cdot kg^{-1}$)	6.5	5.3-7.6	6.4^{ns}	5.5-8.0	13.4	12.4-15.3	12.4^{ns}	11.1-14.1
Glucose ($g \cdot kg^{-1}$)	2.5	2.1-3.1	2.7^{ns}	2.1-3.5	5.5	5.1-6.0	5.3^{ns}	4.7-6.3
Fructose ($g \cdot kg^{-1}$)	3.1	2.8-3.5	2.9^{ns}	2.7-3.4	6.2	5.9-6.4	5.9^{ns}	5.2-6.9
Sucrose ($g \cdot kg^{-1}$)	0.6	0.5-0.8	0.6^{ns}	0.5-0.8	1.3	0.9-1.7	1.0^{ns}	0.9-1.2
Maltose ($g \cdot kg^{-1}$)	0.4	0.0-0.6	0.4^{ns}	0.0-0.6	1.0	0.8-1.2	0.8^{ns}	0.7-0.9
Starch ($g \cdot kg^{-1}$)	24.7	12.9-33.3	31.4^{**}	28.2-33.7	49.2	42.6-54.0	60.2^{***}	51.1-70.9
Fiber ($g \cdot kg^{-1}$)	12.5	11.8-13.5	13.2^{ns}	7.5-24.5	11.3	8.6-13.6	14.2^{ns}	12.6-16.0
Antioxidants								
Total vitamin C ($mg \cdot kg^{-1}$)	54	39-61	47^{***}	40-58	233	168-291	217^{**}	198-252
Ascorbic acid (AA; $mg \cdot kg^{-1}$)	20	18-24	16^{***}	9-20	91	71-125	67^{***}	34-83
Dehydroascorbic acid (DHAA; $mg \cdot kg^{-1}$)	34	21-44	32^{ns}	23-41	142	97-166	150^{ns}	115-169
Total phenolics ($mg \cdot kg^{-1}$)	1014	746-1417	582^{***}	509-712	843	651-1162	627^{***}	547-725

[a] ns, *, **, ***, indicate non-significant ($P \geq 0.05$), and significant at $P<0.05$, $P<0.01$, and $p<0.001$, respectively, for the orthogonal comparison of landraces vs. hybrid cultivars in the GH1 and OF1 seasons.

Table 8.Mid-parent heterosis (%) for the fruit composition traits measured in two environments (open field 2 and greenhouse 2) of three F1 hybrids between three eggplant traditional landraces.

	Open field 2			Greenhouse 2		
Traits	CS16×H11[a]	CS16×IVIA371	H11×IVIA371	CS16×H11	CS16×IVIA371	H11×IVIA371
Proximate traits						
Moisture	-0.17[ns]	-0.55[**]	-1.30[**]	-0.36[ns]	-1.65[***]	-0.18[ns]
Proteins	-7.58[ns]	18.70[ns]	39.85[**]	-18.12[*]	40.54[***]	-21.89[*]
pH	-1.03[ns]	0.28[ns]	0.00[ns]	4.68[ns]	2.06[ns]	0.74[ns]
Titratable acidity (TA)	-16.99[***]	0.66[ns]	13.52[***]	-26.00[***]	8.94[*]	0.03[ns]
Carbohydrates						
Total available carbohydrates (TAC)	7.30[ns]	12.13[ns]	-16.47[*]	13.03*	19.69[**]	24.61[***]
Total soluble sugars (TSS)	-10.33[ns]	-22.79*	-12.35[ns]	-1.79[ns]	1.65[ns]	-3.12[ns]
Glucose	-24.14[ns]	-58.68[***]	-11.04[ns]	5.53[ns]	2.93[ns]	0.78[ns]
Fructose	-7.02[ns]	-15.45[ns]	-8.59[ns]	-9.87[ns]	2.20[ns]	0.00[ns]
Sucrose	-11.54[ns]	116.67[ns]	-28.00[ns]	-31.25[ns]	-35.71[ns]	-25.00[ns]
Maltose	-23.81[ns]	86.68[ns]	18.18[ns]	48.39[ns]	68.00[ns]	0.00[ns]
Starch	35.66[ns]	67.05[**]	-25.98[ns]	37.95[*]	64.55[*]	77.08[**]
Fiber	2.39[ns]	-27.41[ns]	-34.75[*]	23.70[ns]	72.56[***]	40.20[*]
Antioxidants						
Total vitamin C	-24.37[***]	12.37[**]	0.06[ns]	-7.46[**]	26.69[***]	-22.04[***]
Ascorbic acid (AA)	-1.06[ns]	20.43[**]	-2.33[ns]	26.90[***]	27.15[***]	-14.32[**]
Dehydroascorbic acid (DHAA)	-35.35[***]	7.02[ns]	1.41[ns]	-21.32[***]	26.48[***]	-25.26[***]
Total phenolics	1.47[ns]	-2.48[ns]	1.41[ns]	8.95[ns]	5.64[ns]	-1.31[ns]

[a][ns], [*], [**], [***], indicate mid-parent heterosis values non-significant ($P \geq 0.05$), and significant at $P<0.05$, $P<0.01$, and $p<0.001$, respectively.

Figure 1. Fruits of the three eggplant landraces evaluated (situated in the triangle points: CS16, below right; H11 below left; and, IVIA371 above) and of their respective hybrids (situated in the triangle sides between their respective parents; CS16×H11, below center; CS16×IVIA371, right intermediate; and, H11×IVIA371, left intermediate).

Figure 2. Fruits of the three eggplant commercial F1 hybrids evaluated (Bandera, left; Cristal, center; Ecavi, right).

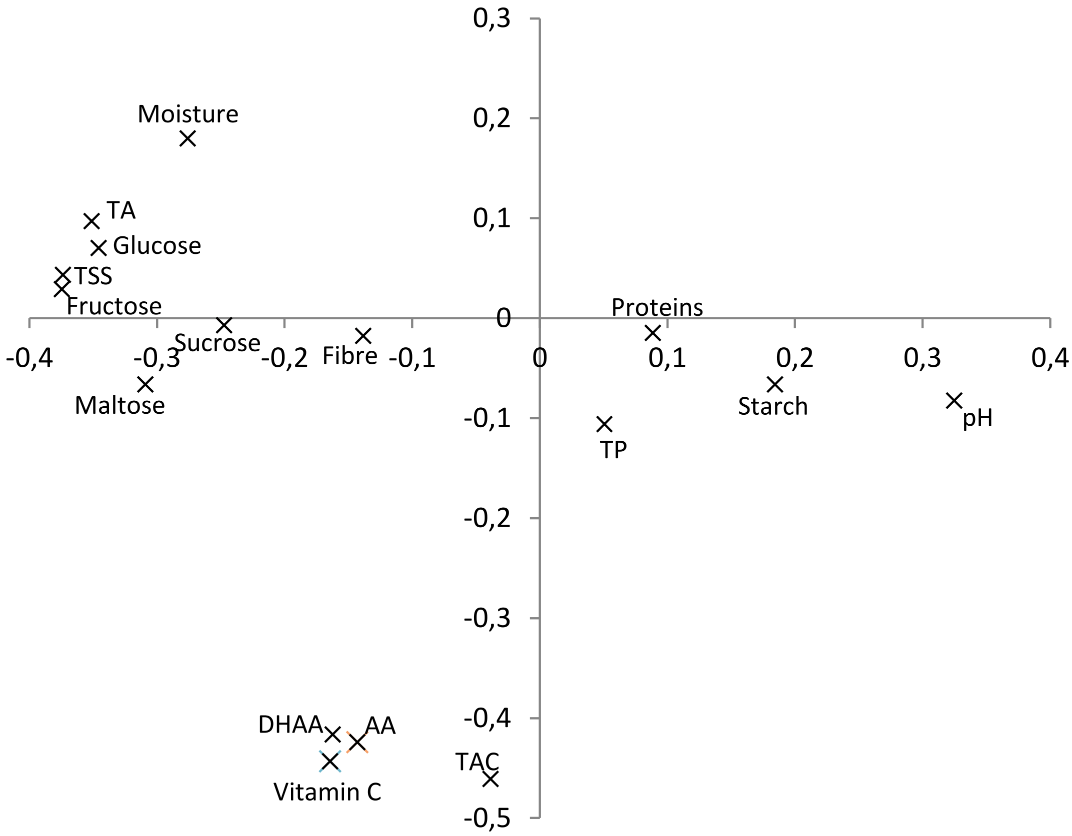

Figure 3. Loading plot of the first and second principal components for the15 eggplant composition traits studied (see Table 2) based on the two principal components of PCA. First (X-axis) and second (Y-axis) components of the PCA account for 42.1% and 24.4% of the total variation, respectively. Results are based on the data obtained from the mean values of three landraces, three commercial F1 hybrids, and the three hybrids between the landraces. Landraces were evaluated over four seasons (two in the open field and two in greenhouse),and commercial F1 hybrids and the hybrids between the landraces over two seasons (one in the open field and one in greenhouse; different seasons for commercial and landrace hybrids).

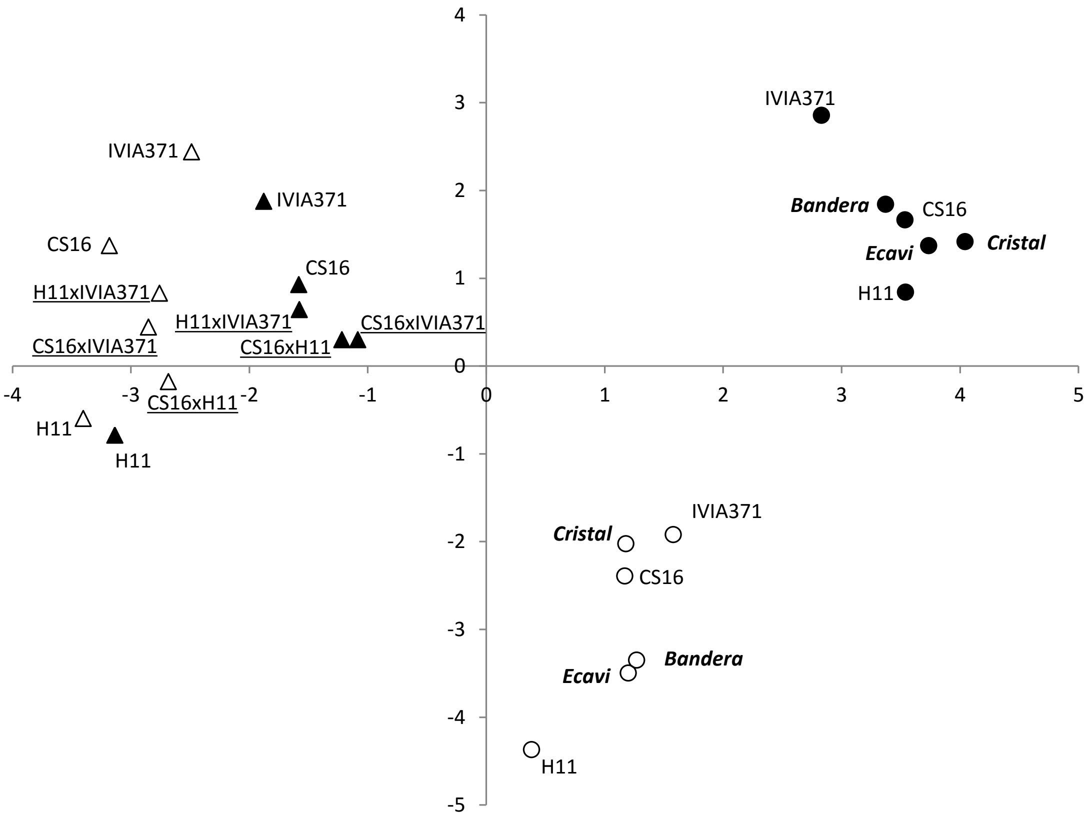

Figure 4. Score plot of the first (X-axis) and second (Y-axis) principal components for the 24 combinations of eggplant genotype and season evaluated based on 15 fruit composition traits (see Table 3).First (X-axis) and second (Y-axis) components of the PCA account for 42.1% and 24.4% of the total variation, respectively. The different seasons are represented by different symbols: Open field 1 (OF1, black circles), Greenhouse 1 (GH1, white circles), Open field 2 (OF2, black triangles), Greenhouse 2 (GH2, white triangles). The different varietal types are indicated using different font types: Landraces (normal font), commercial F1 hybrids (italics bold font), and hybrids between landraces (underlined font).