

Genetics of Orange, Red and Yellow Root Colours in Tropical Carrots (*Dacus Carota* L.)

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Abstract

The research was carried out to study the colour inheritance genetics of the root epidermis, core (phloem) and cortex (xylem), from the parental crosses of the varieties Pusa Meghali (Orange), Pusa Rudhira (Red) and Pusa Kulfi (Yellow). Resultant in crosses yielded uniform mixed colours in F_1 (first filial generation), thus could enhance the security of human nutrition through the mixture of carotenoids and anthocyanins in the F_1 . The F_1 s were advanced to produce F_2 and backcross (BCP_1 and BCP_2) generations, and the Chi-square test ratio (χ^2) showed that the root colour of the orange epidermis and cortex (xylem) was dominant over the red and yellow colours, and regulated by dominant genes *Oe* and *Ocx* from the parent Pusa Meghali. While, the root colour of the orange core (phloem) was found to be recessive to the red (*Rc*) from Pusa Rudhira and yellow (*Yc*) colour from Pusa Kulfi, and to be regulated by a single recessive gene (*oc*) from the parent Pusa Meghali. These findings of genetic inheritance of colours would be useful in the development of bio-fortified F_1 hybrids and varieties which are rich in flavonoids.

Introduction

Carrot (*Daucus carota* L.) first definitive mention as a root crop around 1100 years in central Asia, orange carrots first sighted in southern Europe during 15th century (Stolarczyk and Janick 2011), and red carrots noted Asia in 17th century (Rubatzky et al. 1999; Simon 2000). Orange colour cultivars are predominant in carrots, and cultivars were developed in Europe since from the 16th century (Banga 1963). Carotenoids have been a distinctive feature of carrots, and the colours of carrots were stated either orange and yellow or purple (Banga 1957, 1963; Simon 2000). Wild carrots contain traces of carotenoids, while cultivated carrots contain at most carotenoids (Arscott and Tanumihardjo 2010). Carotenoids are a valuable source of dietetic vitamin A and are a variety of carrot roots of orange, red, and yellow colour, their biosynthesis, development and accumulation differ with diverse environmental and genetic contexts, the carotenoid biosynthetic genes upregulation in carrots yield the high carotenoid content. The interaction of Y and Y_2 genes contribute for the variation of carotenoids in white, yellow, and orange carrots, *Or* gene association with carotenoids of carrot has been acknowledged, and discovery of genes which are contributing to the carotenoids biosynthesis pathway have an exciting consequence for carotenoids rich carrot improvement (Simon et al. 2019). Due to the inability of *de novo* synthesis of carotenoids, humans are aware of the nutritional value of carotenoids, dietary carotenoids (α -carotene, β -carotene, β -cryptoxanthin, lycopene and lutein) converted to vitamin A, which is important for cancer and cardiovascular risk reduction, for the maintenance of immunity, growth and reproduction (Tanumihardjo 2012). The major carotenoids are lutein contributes to the yellow root colour, a- and b-carotene contribute to the orange root colour, and lycopene produces the red colour. (Arscott and Tanumihardjo 2010). Orange carrots contain trace amounts of phytoene, f-carotene, lutein and lycopene (Grassmann et al. 2007; Nicolle et al. 2004; Simon and Wolff 1987), red carrots produce a- and b-carotene, lutein, and lycopene (Arscott and Tanumihardjo 2010; Grassmann et al. 2007), high carotenoid content noted from orange, yellow, and red colour roots (Wang et al. 2014)

Carrot colours were first noted by carrot breeders to reference the cross with wild carrots (white root) during carrot breeding (Vilmorin 1859), cultivated white and yellow carrots intercrosses revealed the white root colour was dominant to yellow root colour (Borthwick and Emsweller 1933; Emsweller et al. 1935), yellow root colour dominant over orange root colour, which was governed by a single dominant gene (Emsweller et al. 1935; Lamprecht and Svensson 1950), orange root colour dominant over red coloured root from the crosses between orange and red coloured carrots, F_2 and backcross populations showed the two genes *A* and *L* were conditioned for lycopene and a-carotene content in progeny (Katsumata et al. 1966). The carrot root colour has been controlled by several genes, white root colour dominant over yellow colour carrot through single dominant gene, the segregation ratios from the crosses between white and orange colour parents yielded white, orange and yellow progenies in F_2 , F_3 and backcrosses fitted in two to three gene patterns of inheritance depending on the population (Laferriere and Gabelman 1968; Imam and Gabelman 1968). Kust (1970) named the white colour controlling single gene *Y* dominant over yellow root colour, and additional two dominant genes Y_1 and Y_2 were revealed from white and orange crosses, the dominant alleles in the crosses white \times yellow, white \times orange and yellow \times orange revealed low carotenoids contents (Laferriere and Gabelman 1968). Natural orange carrot mutant was conditioned by a recessive gene noted as *rp*, reduces root α -, β -carotene, and α -tocopherol content with high phytoene content, and *rp* gene associated with reduced plant vigour, a unique carrot gene associated with carotenoid colour (Goldman and Breitbach 1996; Koch and Goldman 2005). The high heritability of total carotenoid content (0.89–0.98%) noted for the B493 \times QAL, and low heritability was noted from the Brasilia \times HCM (0.38 to 0.45), this indicated *Y* and Y_2 genes largely influence on the cross B494 \times QAL population, and the variability of carotenoids content among the population influence on the environments (Perrin et al. 2016, 2017), the allelic variation for the *Or* gene observed mainly in the centre of diversity of carrots from Central Asia than the European carrots (Iorizzo et al. 2013). The orange carrot (yy_1y_2) and wild yellow carrot (*Orw*) have a homozygous condition of the cross, thus the heterozygotes are light orange (*OrcOrcyy_1y_2*), the variation for *Or* gene evolved during early carrot domestication at Central Asia from wild *Orc* allele (Simon et al 2019). In F_2 population of red \times white crosses intricate a new tinge yellow-red colour phenotype with a high content of total carotenoids in xylem than the phloem, more variability of pigments found in F_2 populations of red \times yellow and red \times white and yet genetics of this phenotype not known (Buishand and Gabelman 1980). In the context of root epidermis, root cortex and root colour inheritance studies were not done so far, hence we have undertaken the study to investigate the inheritance orange, yellow and red colours, since carrot root epidermis, core and cortex colour varied with a single colour to mixed colours, studies are limited and lacking on tropical carrot colour inheritance, thus the genetics of colour inheritance of root epidermis, core and cortex of carrot-based on the systemic colour classification using RHS mini colour chart (RHS 2005), these research findings will be helpful in the development of tropical carrot varieties and F_1 hybrids.

Materials And Methods

Plant materials

The inbred lines of Pusa Asita (purple colour), Pusa Rudhira (red colour), Pusa Kulfi (yellow colour) and Pusa Meghali (orange colour) with a single colour of epidermis, core and cortex were developed in Division of Vegetable Science, Indian Agricultural Research Institute, New Delhi, India. F_1^s (first filial generation) were developed by the crosses inbred lines during 2012–2013, F_1 's were selfed and produced F_2 generations, and backcrosses were developed by crossing both the parents to the corresponding F_1 's during 2014–2015. The F_2 and back cross (BCP_1 and BCP_2) population were used for assessment of carrot root colour inheritance.

Carrot root epidermis, core and cortex colour classification and genetics of inheritance

The field grown carrot plants were harvested by uprooting and washed the roots of different populations (Parents, F_1 , F_2 and Backcross), then the carrot roots were sliced for standard colour evaluation, root colours were evaluated based on Royal Horticultural Society mini chart 2005 (RHS 2005), the root colours were classified and classification is given in Table 1, and the genetics of root colour inheritance was assessed using RHS colour classification. Root epidermis, core and cortex colour of classified F_2 , BCP_1 , and BCP_2 population were analyzed by Chi-square (χ^2) tests for goodness of fit using plant breeders tools (PBT 2005) software which was developed by International Rice Research Institute, the test ratios of phenotypes evaluated were compared with 3:1 for the F_2 , and 1:1 for the BCP_1 and BCP_2 generations respectively.

Table 1
Colour grouping according to the Royal Horticultural Society Mini-Colour Chart (2005)

RHS Code	Colour Chart	Root Colour
RHS-N79A		Red Purple (Dark Purple Red)
RHS-59B		Rose Purple (Dark Brown)
RHS-187A		Black Purple (Dark Purple)
RHS-N77B		Grey Purple (Dark Brown)
RHS-32B		Orange Red
RHS-33A		Light Red
RHS-31A		Orange Pink (Medium Orange Pink)
RHS-34C		Medium Red (Orange Red)
RHS-23C		Yellow Orange (Medium yellow Orange)
RHS-24A		Medium Orange
RHS-25A		Light Orange
RHS-29C		Orange Pink (Medium Orange Pink)
RHS-2C		Yellow Green (Light Yellow Green)
RHS-1D		Light Yellow
RHS-4B		Medium Yellow
RHS-9B		Yellow (Medium Yellow)

Results And Discussion

Inheritance genetics of epidermis, cortex and core root colours

The F_1 hybrids were developed between orange (Pusa Meghali), red (Pusa Rudhira) and yellow (Pusa Kulfi) root coloured carrots had orange epidermis and cortex in the combination of red and yellow root core, and there were no maternal effects were found on epidermis and cortex root colours from the parents of reciprocal crosses. This could be due to the dominant gene action of orange root epidermis (*Oe*) and cortex (*Ocx*) contributed from the inbred parent Pusa Meghali, and root core colour influenced by the dominant genes *Rc* from Pusa rudhia and *Yc* from Pusa Kulfi. The orange carrot (yy_2y_2) and wild yellow carrot (*Orw*) have the homozygous condition of a cross, thus the heterozygotes are light orange (*OrcOrcyy_2y_2*), the variation for *Or* gene evolved during early carrot domestication at Central Asia from wild *Orc* allele (Simon et al 2019). The single dominant genes governing traits are valuable assets in the exploitation of heterosis for root yield enriched with high carotenoids content.

The segregation of the F_2 population of the cross Pusa Meghali (Orange root) × Pusa Rudhira (Redroot), the backcross population of (Pusa Meghali × Pusa Rudhira) × Pusa Meghali (BCP₁) and (Pusa Meghali × Pusa Rudhira) × Pusa Rudhira (BCP₂), and the F_2 population of the cross Pusa Rudhira × Pusa Meghali, the backcross population of (Pusa Rudhira × Pusa Meghali) × Pusa Rudhira (BCP₁), (Pusa Rudhira × Pusa Meghali) × Pusa Meghali (BCP₂) population presented in Table 2, the test ratio was fitted in the goodness of Chi-square test revealed the orange epidermis (*Oe*) and cortex (*Ocx*) colour dominant over red (*re*, *rcx*) colour with the genetics of inheritance governed by single dominant gene pattern for the orange epidermis and cortex colour of carrot root. Whereas the orange root core (*oc*) colour was recessive to the red (*Rc*) colour, test ratio findings showed that the orange core colour of the root was regulated by the single recessive gene (Fig. 1), orange root colour dominant over red coloured root from the crosses between orange and red coloured carrots, F_2 and backcross populations showed the two genes *A* and *L* were conditioned for lycopene and a-carotene content in progeny (Katsumata et al. 1966). Natural orange carrot mutant was conditioned by a recessive gene noted as *rp*, reduces root α -, β -carotene, and α -tocopherol content with high phytoene content, and *rp* gene associated with reduced plant vigour, a unique carrot gene associated with carotenoid colour (Goldman and Breitbach 1996; Koch and Goldman 2005). In F_2 population of red × white crosses intricate a new tinge yellow-red colour phenotype with a high content of total carotenoids in xylem than the phloem, more variability of pigments found in F_2 populations of red × yellow and red × white and yet genetics of this phenotype not known (Buishand and Gabelman 1980). Interestingly, the characteristic coexistence of yellow and orange colour in the roots, the colour assorted in different root sections with unique stoichiometry could be assigned to different parents in the genetic backgrounds was fairly explained by simple inheritance for root epidermis, cortex and core colour of carrot root of the inbred parents Pusa Meghali and Pusa Rudhira.

Table 2
Root colour segregation and inheritance of population developed from Pusa Maghali and Pusa Rudhira

Pusa Maghali (P ₁) × Pusa Rudhira (P ₂)													
Population	Traits	Yellow Orange	Medium Orange	Light Orange	Orange Pink	Orange Red	Light Red	Orange	Red	Total	Test Ratio	χ ²	P
F ₂	Epiderm	106	71	52	92	39	69	321	108	429	2.97:0.34	0.00	0.93
BCP ₁	Epiderm	23	11	10	18	18	39	62	57	119	1.09:0.92	0.21	0.64
BCP ₂	Epiderm	10	16	10	16	28	37	52	65	117	0.80:1.25	1.44	0.22
F ₂	Cortex	94	53	61	88	43	60	296	103	429	2.87:0.35	0.14	0.70
BCP ₁	Cortex	18	22	12	10	48	9	62	57	119	1.09:0.92	0.21	0.64
BCP ₂	Cortex	18	19	14	12	29	24	63	54	117	1.17:0.86	0.69	0.40
Population	Traits	Orange Red	Light Red	Orange Pink	Medium Red	Yellow Orange	Medium Orange	Orange	Red	Total	Test Ratio	χ ²	P
F ₂	Core	99	97	62	94	67	60	127	352	429	0.36:2.77	0.58	0.04
BCP ₁	Core	18	14	13	13	43	18	61	58	119	1.05:0.95	0.07	0.78
BCP ₂	Core	16	19	14	12	32	24	56	61	117	0.92:1.09	0.21	0.64
Pusa Rudhira (P ₁) × Pusa Maghali (P ₂)													
Population	Traits	Yellow Orange	Medium Orange	Light Orange	Orange Pink	Orange Red	Light Red	Orange	Red	Total	Test Ratio	χ ²	P
F ₂	Epiderm	117	78	57	63	42	65	315	107	422	2.94:0.34	0.02	0.86
BCP ₁	Epiderm	22	14	10	15	25	32	61	57	118	1.07:0.93	0.13	0.71
BCP ₂	Epiderm	23	15	10	11	20	35	59	55	114	1.07:0.93	0.14	0.70
F ₂	Cortex	137	62	96	47	58	63	342	121	422	2.83:0.47	0.31	0.57
BCP ₁	Cortex	15	18	11	12	42	20	56	62	118	0.90:1.11	0.30	0.58
BCP ₂	Cortex	22	13	15	9	41	14	59	55	114	1.07:0.93	0.14	0.70
Population	Traits	Orange Red	Light Red	Orange Pink	Medium Red	Yellow Orange	Medium Orange	Orange	Red	Total	Test Ratio	χ ²	P
F ₂	Core	98	77	64	69	54	60	114	308	422	0.37:2.70	0.91	0.33
BCP ₁	Core	19	12	16	10	37	24	61	57	118	1.07:0.93	0.13	0.71
BCP ₂	Core	15	14	18	13	41	13	54	60	114	0.90:1.11	0.31	0.57

The F₂ segregates of the cross Pusa Kulfi (Yellow root) × Pusa Meghali (Orange root), the backcross population of (Pusa Kulfi × Pusa Meghali) × Pusa Kulfi (BCP₁), (Pusa Kulfi × Pusa Meghali) × Pusa Meghali (BCP₂), and the F₂ population developed from the cross Pusa Meghali × Pusa Kulfi, (Pusa Meghali × Pusa Kulfi) × Pusa Meghali (BCP₁) and (Pusa Meghali × Pusa Kulfi) × Pusa Kulfi (BCP₂) populations presented in Table 3, the goodness of fit Chi-square test ratio revealed the orange epidermis (*Oe*) and cortex (*Ocx*) colour dominant over yellow (*ycx*) colour and governed by single dominant genes. Whereas, the orange root core (*oc*) colour was recessive to the yellow core (*Yc*) colour of root, and orange core colour of carrot root governed by the single recessive gene (Fig. 2). The segregating population of carrot crosses between red and yellow colour roots inferred three major genes, namely carotenoid synthesis inhibitor (*Y*₂), lycopene synthesis stimulator (*L*) and dominant gene responsible for β- and α-carotene at the expense of lycopene could yield high orange colour root rich in carotenes resulted from red colour roots, furthermore the possible interaction of minor and modifier gene interactions, and two inhibitor genes (*Y* and *Y*₂) were segregated from the crosses between red and white colours, In F₂ population of red × white crosses intricate a new tinge yellow-red colour phenotype with high content of total carotenoids in xylem than the phloem, more variability of pigments found in F₂ populations of red × yellow and red × white (Buishand and Gabelman 1980), In the F₂ population of the cross red × white revealed two genes could have involved in the segregation of yellow colour progenies Kust (1970), the white color controlling single gene *Y* dominant over yellow

root colour, and additional two dominant genes Y_1 and Y_2 were revealed from white and orange crosses, the dominant alleles in the crosses white × yellow, white × orange and yellow × orange revealed low carotenoids contents (Laferriere and Gabelman 1968). The allelic tests among inbreds (yellow root) yielded cent per cent yellow roots in the F_2 population, with minimum white cores (PI175719 × PI220285). The F_2 population of the cross PI173687 × *Rheinische* were all yellow rooted plants thus root colours governed by Y_2 , because *Rheinische* segregant of Y_2/Y_2 (Buishand and Gabelman 1979), yellow root colour dominant over orange root colour, which was governed by a single dominant gene (Emsweller et al. 1935; Lamprecht and Svensson 1950), this indicated Y and Y_2 genes largely influence on the cross B494 × QAL population, and the variability of carotenoids content among the population influence on the environments (Perrin et al. 2016, 2017). The co-occurrence of yellow and orange colour in the roots are the interesting traits, since the assortment of colour in the different root part with specific stoichiometry, could be attributed by different parents was relatively explicated simple genetic inheritance for root epidermis, cortex and core colour of carrot root in genetic backgrounds of Pusa Kulfi and Pusa Meghali parents.

Table 3
Root colour segregation and inheritance of population developed from Pusa Kulfi and Pusa Meghali

Pusa Kulfi (P_1) × Pusa Meghali (P_2)													
Population	Traits	Yellow Orange	Medium Orange	Light Orange	Orange Pink	Yellow Green	Light Yellow	Orange	Yellow	Total	Test Ratio	χ^2	P
F_2	Epiderm	112	66	62	78	66	47	318	113	431	2.81:0.36	0.34	0.55
BCP ₁	Epiderm	23	12	16	14	20	34	65	54	119	1.20:0.83	1.01	0.31
BCP ₂	Epiderm	27	14	10	10	35	23	61	58	119	1.05:0.95	0.07	0.78
F_2	Cortex	101	64	58	98	46	64	321	110	431	2.92:0.34	0.06	0.80
BCP ₁	Cortex	19	10	17	11	21	41	57	62	119	0.92:1.09	0.21	0.64
BCP ₂	Cortex	21	12	12	9	32	33	54	65	119	0.83:1.20	1.01	0.31
Population	Traits	Yellow Green	Light Yellow	Medium Yellow	Yellow	Yellow Orange	Medium Orange	Orange	Yellow	Total	Test Ratio	χ^2	P
F_2	Core	118	54	57	68	76	58	134	297	431	0.45:2.22	0.06	0.80
BCP ₁	Core	20	11	14	12	28	34	62	57	119	1.09:0.92	0.21	0.64
BCP ₂	Core	24	16	13	14	34	18	52	67	119	0.78:1.29	1.01	0.31
Pusa Meghali (P_1) × Pusa Kulfi (P_2)													
Population	Traits	Yellow Orange	Medium Orange	Light Orange	Orange Pink	Yellow Green	Light Yellow	Orange	Yellow	Total	Test Ratio	χ^2	P
F_2	Epiderm	107	64	51	84	47	73	306	306	426	2.55:0.39	0.86	0.35
BCP ₁	Epiderm	17	12	18	6	33	25	53	53	111	0.91:1.09	0.22	0.63
BCP ₂	Epiderm	20	10	9	17	22	37	56	60	115	0.95:1.05	0.07	0.77
F_2	Cortex	114	55	67	82	46	62	318	108	426	2.94:0.34	0.02	0.86
BCP ₁	Cortex	10	18	14	10	21	38	52	59	111	0.88:1.13	0.44	0.50
BCP ₂	Cortex	18	13	11	14	24	35	56	59	115	0.95:1.05	0.07	0.77
Population	Traits	Yellow Green	Light Yellow	Medium Yellow	Yellow	Yellow Orange	Medium Orange	Orange	Yellow	Total	Test Ratio	χ^2	P
F_2	Core	107	64	51	84	47	73	120	306	426	0.39:2.55	2.28	0.13
BCP ₁	Core	17	12	18	6	33	25	58	53	111	1.09:0.91	0.22	0.63
BCP ₂	Core	21	16	14	9	29	26	55	60	115	0.92:1.09	0.21	0.64

Conclusion

Cultivated carrot yield diverse carotenoids due to colours assortment in the root aided with the interaction of several genes, the diverse root colours namely orange, yellow and red are associated in the accumulation of carotenoids in the root. It is challenging to compare colours attributed to carotenoid content in the mixed colour segregated in the root, and complex task to understand the cause for variation of mixed carotenoids in the root. To account the causal genes for the variability of carotenoids in the epidermis, cortex and core based on the chi-square test ratio of segregating population were ascertained that the dominant genes are *Oe* (orange epidermis) and *Ocx* (orange cortex) from Pusa Meghli, *Yc* (yellow core) from Pusa Kulfi and *Rc* (red core) from Pusa Rudhira, recessive genes namely *oc* (orange core) from Pusa Meghli, *ye* (yellow epidermis) from Pusa Kulfi, *re* (red epidermis) from Pusa Rudhira, *yc* (yellow cortex) from Pusa Kulfi and *rc* (red cortex) Pusa Rudhira were possibly responsible for an assortment of root colour in F_1 , F_2 , and backcross population. The genetics of root epidermis, cortex and core colour inheritance useful in the accelerating breeding of carotenoids rich varieties and F_1 hybrids with uniform mixed root colours.

Abbreviations

F_1 : First filial generation

F_2 : Second filial generation of segregating population

BCP_1 : Backcross with the male parent to F_1

BCP_2 : Backcross with the female parent to F_1

χ^2 : Chi-square test ratio

Ocx: Orange cortex controlled by a dominant gene

Oe: Orange epidermis controlled by a dominant gene

Oc: Orange core controlled by a dominant gene

oc: Orange epidermis controlled by a recessive gene

Rc: Red core controlled by a dominant gene

re: Red core controlled by a recessive gene

rcx: Red cortex controlled by a recessive gene

Yc: Yellow core controlled by a dominant gene

ycx: Yellow cortex controlled by a recessive gene

Declarations

Compliance with ethical standards

Ethical Statement

The manuscript was not submitted elsewhere, and results were presented without falsification, fabrication, or inappropriate data manipulation. Research does not pose any threat to public health or national security.

Conflicts of interest

We the authors declare no competing interest with the manuscript

Data disposition statement

Availability of data and material

The means of experimental data were presented in the form of tables and the inference interpreted in the manuscript. The parental lines and breeding population are available with first author; seed request for research purpose may post to the first author through proper channel.

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Figures

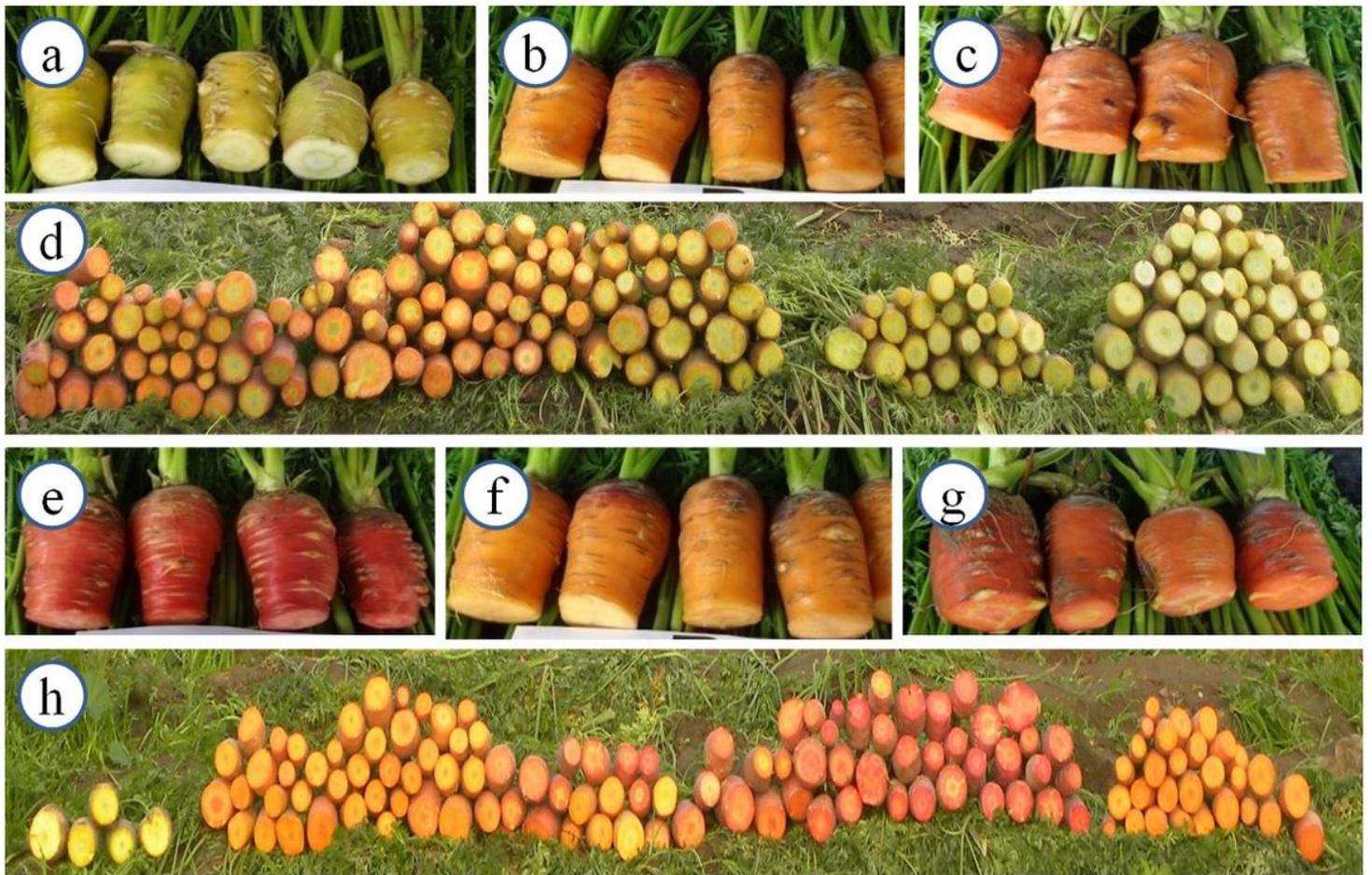


Figure 1

a) Puas Kulfi, b) Puas Meghali, c) F1 Hybrid of Puas Kulfi × Puas Meghali, d) F2 population developed from the cross Puas Kulfi × Puas Meghali, e) Puas Rudhira, f) Puas Meghali, g) F1 Hybrid of Puas Rudhira × Puas Meghali, h) F2 population developed from the cross Puas Rudhira × Puas Meghali

Image not available with this version

Figure 2