Phenotypic Plasticity of Vegetable Amaranth, *Amaranthus tricolor* L. under a Natural Climate

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Abstract: The plastic responses of fifteen *Amaranthus tricolor* L. cultivars to the natural climatic conditions across successive two years were investigated. The interactions between cultivars and climates showed significant effects on all variables examined. SAT-072 cultivar showed the lowest plasticity in both years. Principle component analysis revealed three components (PCs) associated with 67% of the total variation (PC1 = 36%, PC2 = 19%, PC3 = 12%). PC1 includes leaf color attribute *a**(red pigment)*, and photosynthetic pigments (chlorophyll a, chlororphyll b, total chlorophyll), while PC2 accounts for leaf color attribute *b**(yellow pigment), betacyanins, betaxanthins and betalains. Canonical discriminant analysis (CDA) was an effective method for clear separation or grouping of cultivars that may promote effective management and utilization in crop-breeding programmes. Overall, these findings suggest the necessity of further study to enrich amaranth cultivars with desirable traits.

Key words: *Amaranthus tricolor* L., Canonical discriminant analysis, Functional variables, Phenotypic plasticity, Principle component analysis.

Amaranth is an excellent versatile crop which can grow over a wide range of agro-climatic zones showing resistance to different environmental stresses and thereby may readily adapt to new environments (Brenner et al., 2000; Rana et al., 2007). As a multi-purpose crop, some of the amaranths are popular as leafy vegetables with high nutrient values both for humans and animals (Mlakar et al., 2009; Khanam et al., 2012; Khanam and Oba, 2013) while some others are cultivated as grain amaranth. In addition, amaranths having attractive inflorescence and leaf color are grown as ornamental plants (Mlakar et al., 2009). In these context, amaranth has drawn huge research interest for its antioxidants and other medicinal (antimalarial, antiviral etc.) properties (Maharwal et al., 2005; Hilou et al., 2006; Roy et al., 2006). However, recent studies on the C4 photosynthetic pathway, wide genetic diversity and phenotypic plasticity of amaranth suggest the necessity to explore the influence of environmental factors on amaranth crop (Shukla et al., 2010).

The vegetable amaranth, *Amaranthus tricolor* L. seems to have originated from South or Southeast Asia (Grubben and van Sloten, 1981) and consequently dispersed across tropical as well as temperate zones (Martin and Telek, 1979). Recent studies indicate that the varieties of *A. tricolor* are important sources of bioactive compounds such as polyphenols, flavonoids (Khanam and Oba, 2013), vitamins and pigments such as betalains and carotenoids (Sokkanha and Tiratanakul, 2006). Betalains coexist with an attractive color, beneficial bioactivity, health promoting properties, good performance in food processing and taxonomic significance (Han et al., 2009) in vegetable amaranth. They are water-soluble nitrogenous compound and also occur in other plants of Caryophyllales order. According to the chemical structures, betalains are classified as betaxanthins which appear yellow and orange and as betacyanins which appear red to purple (Hendry and Houghton, 1996).

Environmental variation may provoke a variety of changes within a species. Phenotypic plasticity is the ability of an organism to change its phenotype in response to changes in the environment (Price et al., 2003). Climatic variation in successive years may stand for such an alteration and a species needs to adjust to any novel condition for its survival (Nicotra et al., 2010). Phenotypic plasticity thus could become essential for the existence of an organism (Bradshaw, 1965; Sultan, 1992; Pintado et al., 1997). Studies on evolution in a heterogeneous environment usually deal with different aspects of a reaction norm, a set of phenotypes produced by an individual in response to different environments (Schnulgausen, 1949). Phenotypic plasticity in several plant traits has been postulated as a new approach which may represent even specialization (Lortie and Aarssen, 1996). However, plasticity increases in favorable environments and decreases in less favorable environments (Valladares et al., 2000).

To date, *A. tricolor* L. (Amaranthaceae: Caryophyllales) is an underexploited crop. (Jansen, 2004). In this study, we
investigated the phenotypic plasticity in functional variables of fifteen *A. tricolor* cultivars under natural climatic conditions: temperature, rainfall, humidity and sunlight. The functional variables include: leaf color attributes such as $L^*$ (values indicate brightness or lightness), $a^*$ (“+” and “-” values for redness and greenness), and $b^*$ (“+” and “-” values for yellowness and blueness), leaf chlorophyll contents, betalains as well as betacyanins and betaxanthins content, plant height and plant biomass. The aims of this research are: to examine the phenotypic plasticity in 13 functional variables of the amaranth cultivars to a natural climate considering 13 functional variables, and to detect variation in such plasticity and thereby identify and separate the groups of cultivars for their effective management and proper utilization in future breeding programs.

**Materials and Methods**

1. **Plant material and experiment design**

The study was conducted with fifteen *A. tricolor* L. cultivars: six from Bangladesh (Rocto alta, Alto pati, Rocto ranga, Baromashi, BARI-1, SAT-072), four from Asian Vegetables Research and Development Centre (AVRDC), Taiwan (TOT0521, TOT4660, TOT4266 A, TOT2365) and five from Vietnam (Rau den (1), Rau den (2), Rau den (3), Rau den do, Den 3 mau trang nong). The seeds of each cultivar were sown in an incubator at 30°C on 1 June 2010 and June 2011. The seedlings were transplanted to the field at the Gifu Field Science Center, Gifu University (35°27’50.59”N latitude and 136°44’20.15”E longitude) in mid June of both years. The experiment followed a complete randomized block design (CRDB) with three replications. In each replication of a cultivar, 10 seedlings were transplanted into a plot (2 m × 4 m), from which three sample seedlings were randomly selected. Chemical fertilizers and pesticides were not applied in this study. When the plants reached the edible stage (4 weeks after transplanting) 20 fresh leaves per cultivar were hand harvested from the middle portion of the plants.

2. **Leaf color attributes ($L^*$, $a^*$, $b^*$)**

The leaf color attributes $L^*$, $a^*$ and $b^*$ of fresh amaranth leaves were measured using a colorimeter (CS-Sharpner, Toppan, Japan) with 20 replications.

3. **Determination of chlorophyll content**

Chlorophyll $a$ (Chl $a$), chlorophyll $b$ (Chl $b$), and total chlorophyll (Chl) content were determined from 96% ethanolic extracts of fresh amaranth leaves following Lichenthaler and Wellburn, 1983 method using the spectrophotometer (Hitachi, U-1800, Tokyo, Japan) at 665 and 649 nm for chlorophyll $a$ and chlorophyll $b$, respectively.

4. **Determination of betacyanins and betaxanthins**

Betacyanins and betaxanthins were extracted from fresh amaranth leaves using 80% methanol containing 50 mM ascorbic acid according to Wyler et al. (1959) and Girod and Zryd (1991), respectively, were measured spectrophotometrically at 540 and 475 nm, respectively. The quantifications were done using mean molar extinction coefficient ($\epsilon$), which were $62 \times 10^3$ cm$^2$ mol$^{-1}$ for betacyanin and $48 \times 10^3$ cm$^2$ mol$^{-1}$ for betaxanthins. The results were expressed as nanogram betacin equivalent per gram fresh weight (FW) for betacyanins and nanogram indicaxanthin equivalent per gram FW for betaxanthins. The total amount of betalains was calculated from the amount of total betacyanins and betaxanthins.

5. **Measurement of plant height and plant biomass**

The height (cm) of each amaranth plant was measured from ground level to tip of inflorescence when the plants reached the edible stage (4 weeks after transplanting). Five plants per plot were randomly selected, harvested by cutting to ground level and weighted immediately. The plants were dried at 80°C for approx. 48 hours in an electric oven (DRN620DB, Advantec) until they reached constant weight (dry weight). Plant biomass was shown by the percentage of dry weight to fresh weight (%).

6. **Phenotypic plasticity index**

Considering the observed variation in each variable across 2010 and 2011 phenotypic plasticity index (PPI) was calculated. For each cultivar PPI was obtained by using the following equation (Valladares et al., 2000):

$$\text{PPI} = \frac{\text{maximum mean value} - \text{minimum mean value}}{\text{maximum mean value}}$$

Here, mean value for each variable was obtained from the values of three individuals per cultivar. Moreover, mean plasticity index (MPI) of each cultivar was calculated by averaging the plasticity indices obtained for 13 variables and MPI of each variable was calculated by averaging the plasticity indices obtained for 15 cultivars. Correlation of each variable was obtained against the average of MPI of 15 cultivars.

7. **Principle Component and Canonical Discriminant analyses**

Principle component analysis (PCA) was done to assess the patterns of variation in the 13 variables. PCA was applied to analyze and express the variables in such a way as to highlight their similarities and differences. Canonical discriminant analysis (CDA) was applied to derive canonical variables (linear combinations of the variables) that had the highest possible multiple correlation with the groups. CDA is a dimension reduction technique related to PCA but summarize between-class variation (Ye and Robbins, 2004).
8. Statistical analyses

Statistical analyses were conducted using R package (GNU, free software; R Development Core Team, 2010).

Results

1. Plasticity indices

Phenotypic expressions in most of the functional variables of amaranth cultivars appeared to be substantially influenced by the climatic factors (Table 1, 2, Fig.1). The cultivars expressed considerable differences in 13 variables and their phenotypic plasticity indices ranged from 0.16 to 0.45 (Fig. 2a), where SAT-072 cultivar showed the lowest plasticity. Mean plasticity indices (MPI) of leaf color attributes $L^*$, $a^*$ and $b^*$ appeared to be 0.056, 0.42, and 0.57, respectively (Fig. 2b) where $L^*$ showed a lower correlation with MPI of the cultivars ($R^2 = 0.09$) than $a^*$ ($R^2 = 0.35$) and $b^*$ ($R^2 = 0.38$). MPI of photosynthetic pigments exhibited higher correlations with MPI of all cultivars: chlorophyll $a$ (MPI = 0.76, $R^2 = 0.77$), chlorophyll $b$ (MPI = 0.53, $R^2 = 0.64$), total chlorophyll (MPI = 0.67, $R^2 = 0.73$) and Chlorophyll $a/b$ (MPI = 0.56, $R^2 = 0.53$). A lower correlation was observed among MPI of other variables: betacyanins (MPI = 0.31, $R^2 = 0.09$), betaxanthins (MPI = 0.26, $R^2 = 0.01$), betalains (MPI = 0.24, $R^2 = 0.037$), betacyanins/betaxanthins (MPI = 0.35, $R^2 = 0.11$), Plant height (MPI = 0.21, $R^2 = 0.002$) and plant biomass (MPI = 0.19, $R^2 = 0.11$) and among MPI of each cultivar.

Analysis of variance showed significant differences among cultivars over their functional variables in response to the natural climatic conditions across 2010 and 2011 (Table 2). The effect of climatic conditions appeared to be significant over all the variables. Significant interactions were also observed between the cultivars and climatic factors against the variables.

2. Principle Component analysis (PCA)

Principle component analysis (PCA) was simultaneously done to assess the patterns of variations considering all the variables. PCA reduced the dimension of the dataset, inferring a first component with maximal variance and then second component with maximal variance among all components perpendicular to the first, and so on. The first three principle components (PC1, PC2 and PC3) exhibited 67% of the total variation present among 15 cultivars with

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### Table 1. Meteorological data at Gifu University, Japan collected by Japan Meteorological Agency.

| Month / Year | Temperature (°C) | Rainfall (mm) | Humidity (%) | Sunlight (h) |
|--------------|------------------|---------------|--------------|--------------|
| June / 2010  | 23.93            | 17.13         | 66.40        | 5.58         |
| July / 2010  | 27.82            | 19.28         | 68.61        | 6.21         |
| June / 2011  | 23.73            | 9.52          | 68.77        | 4.49         |
| July / 2011  | 27.63            | 10.96         | 67.32        | 5.69         |

### Table 2. ANOVA of the 13 selected functional variables with cultivars and climates.

| Variables | Source of variation | Cultivars $(df = 14)$ | Climate $(df = 1)$ | Cultivars × Climate $(df = 14)$ |
|-----------|---------------------|-----------------------|-------------------|-------------------------------|
| $L^*$     | 778.90***           | 3.68**                | 1060.00***        |
| $a^*$     | 94.98***            | 27.63***              | 396.40***         |
| $b^*$     | 288.20***           | 10.71***              | 837.90***         |
| Chl $a$   | 2.34**              | 220.70***             | 156.50***         |
| Chl $b$   | 1.20 ns             | 358.40***             | 132.10***         |
| Chl $a/b$ | 4.85***             | 62.86***              | 16.73***          |
| Chl       | 1.73*               | 287.00***             | 149.28***         |
| Bc        | 41.07***            | 10.57***              | 137.70***         |
| Bx        | 18.94***            | 8.12***               | 33.31***          |
| Bt        | 43.31***            | 3.11**                | 99.97***          |
| Bc/Bx     | 31.17***            | 17.03***              | 63.91***          |
| PH        | 22.82***            | 11.73***              | 88.03***          |
| BM        | 8.83***             | 4.90**                | 10.91***          |

Fifteen cultivars, 13 functional variables and 2 years climate data (temperature, rain fall, humidity and sunlight) are compared. Table entries are $F$ values. df degree of freedom, *** $P < 0.001$, ** $P < 0.01$, * $P < 0.05$ and ns not significant. $L^*$: lightness, $a^*$: redness/greenness, $b^*$: yellowness/blueness. Chl: Chlorophyll, Bc: Betacyanin, Bx: betaxanthin, Bt: betalain, PH: plant height, BM: % bio mass.
Fig. 1. Phenotypic expression of *A. tricolor* cultivars in two years (2010 and 2011) under natural climates. $L^*$, brightness; $a^*$, (+) redness/(-) greenness; $b^*$, (+) yellowness/(-) blueness; Chl, chlorophyll; Bc, betacyanins; Bx, betaxanthins.
Across a range of environments a species likely evolve different strategies (e.g., specialisation, generalisation, bet-hedging, phenotypic plasticity etc.) for its survival (Dewitt and Langerhans, 2004). Over the environmental changes phenotypic plasticity widely describes all phenotypic responses whereas specialisation induces a single phenotype against a particular environment, generalisation initiates a general phenotype for moderate fitness in most of the environments and bet-hedging triggers either a single or several phenotypes. In our study, all the cultivars, except SAT-072, exhibited considerable plasticity under natural climate in successive years (Fig 1, 2). Thereby SAT-072 cultivar showed lower plasticity i.e., very little changes in response to climatic fluctuations indicating more adaptive phenotypic constancy in adverse environments (Valladares et al., 2000).

In recent years, plant species have been categorized over their functional types. Several plant functional traits have

![Graph](image1.png)

**Fig. 2.** (a) Mean phenotypic plasticity of *A. tricolor* cultivars based on functional variables (b) mean plasticity of thirteen functional variables in *A. tricolor*. $R^2$ showed the coefficient of determination value between each of the functional variables and the mean plasticity of cultivars.

13 variables (Table 3). PC1 extracted 36% of the variation with leaf color attributes $a^*$ value, photosynthetic pigments (chlorophyll $a$, chlorophyll $b$, chlorophyll $a/b$ and total chlorophyll content) and other variables (betacyanins/betaxanthins content) having the largest positive coefficients whereas % biomass showed negative coefficient. PC2 indicated 19% variation with leaf color attribute $b^*$, betacyanins and betalains while betaxanthins showed negative coefficient. Finally PC3 covered 12% variation with lightness value ($L^*$) and plant height.

### 3. Canonical Discriminant analyses (CDA)

Canonical discriminant analysis created two canonical variables Can 1 (33.9%) and Can 2 (25.6%) which exhibited 59.5% of total variations with 13 variables and provided a clear separation among the cultivars (Fig 3). SAT072 cultivar showed the largest positive coefficient with canonical variable 1 (33.9%).

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In recent years, plant species have been categorized over their functional types. Several plant functional traits have
been identified to continue their variation in predictable ways along with the environmental gradients (Nicotra et al., 2010). Thus, the ecology of a species can be described by the functional traits using a few, easily quantified variables (e.g., seed size, plant height, leaf lifespan, leaf mass per area.) (Cornelissen et al., 2003). In global climate models, species are widely grouped in their ecosystem or community according to the variations of their functional types (e.g., C3 or C4 grasses, herbs, shrubs, deciduous trees, N-fixing legumes, etc.) (Nicotra et al., 2010). In this study all of the variables of *Amaranthus tricolor* cultivars showed significant responses to climatic variations in successive years (Table 2). Thus, environmental factors (temperature, rainfall, humidity and sunlight) could influence most of the plant variables in a complex way resulting in their plastic responses. However, more research is needed the other crops. In a study on congeneric shrubs from a panamian rainforest, light affected the phenotypic expression of most variables (Valladares et al., 2000).

In the present study, PCA exhibited the first three PCs with 67% of the total variation encountered among the cultivars taking into account all 13 functional variables simultaneously. PC1 distinguished the cultivars having sufficient red leaf color (*a*), and photosynthetic pigments. The cost effectiveness of the production of amaranth leaves increases as the red color increases. Studies on *A. tricolor* showed that chlorophyll content and ascorbic acid are the major contributing traits of PC1 (Shukla et al., 2010). Chlorophyll content may affect foliage yield with the increment of photosynthetic rate by increasing the vegetative growth of amaranth (Shukla et al., 2006). In contrast, PC2 extracted the cultivars under leaf color *b* value, betacyanins and betalains content. Betalains are water soluble, nitrogen-containing heterocyclic compounds. Betalains of *Amaranthaceae* demonstrate very strong antioxidant activity and thereby could be used as natural antioxidants and colorants (Cai et al., 2003). However, on the basis of lightness value (*L* *) and plant height amaranth cultivars have been distinguished in PC3.

CDA analysis exhibited 59.5% of total variations throughout the experiment and showed a clear separations or grouping of the cultivars. SAT-072 exhibited a clear separation from the other cultivars (Fig. 3) and was positive on canonical variable 1. Rocto alta and Rau den (3) were also plotted on positive portion of canonical variable 1. This grouping indicates that SAT-072 did not show any variation across the climatic conditions of the successive years and thereby showed the highest stability among the cultivars. Rocto alta and Rau den (3) demonstrated the second stable priority among the cultivars under similar natural climatic conditions.

In this study, SAT-072 appears to be the most specialized cultivar with reduced plasticity in all functional variables. Most of the cultivars contained the phenotypic plasticity across the observed years. Photosynthetic pigments exhibited high plasticity under a natural climate. All the functional variables appeared to be unstable suggesting that they are significantly affected with the climatic changes. PCA analysis provided three PCs and encountered photosynthetic pigment as the major functional variations. CDA analysis effectively separated the cultivars in different groups and thereby may facilitate the selection of appropriate cultivars for breeding programs in developing cultivars with desired traits e.g., high-photosynthetic pigments in relation to the influence of climatic factors.

| Variable                  | PC1   | PC2   | PC3   |
|---------------------------|-------|-------|-------|
| Standard deviation        | 2.17  | 1.56  | 1.27  |
| Eigen values              | 4.69  | 2.40  | 1.53  |
| Proportion of Variance    | 0.36  | 0.19  | 0.12  |
| Cumulative proportion     | 0.36  | 0.55  | 0.67  |
| Factor loading            |       |       |       |
| L*(Lightness)             | 0.70  |       |       |
| a*(red/greenness)         | 0.66  |       |       |
| b*(yellow/blueness)       | 0.87  |       |       |
| Chlorophyll a             | 0.96  |       |       |
| Chlorophyll b             | 0.93  |       |       |
| Chlorophyll a/b           | 0.83  |       |       |
| Total chlorophyll         | 0.97  |       |       |
| Betacyanins               | 0.92  |       |       |
| Betaxanthins              | -0.67 |       |       |
| Betalains                 | 0.52  |       |       |
| Betacyanins/Betaxanthins  | 0.42  |       |       |
| Plant height              | 0.49  |       |       |
| % biomass                 | -0.65 |       |       |

Table 3. Principal Component analysis of 13 functional variables in 15 cultivars.
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