DIFFERENTIAL RESPONSES OF CERTAIN ETHIOPIAN GROUNDNUT
(*Arachis hypogaea* L.) VARIETIES VARYING IN DROUGHT TOLERANCE,
TO TERMINAL DROUGHT STRESS

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Received – February 05, 2020; Revision – March 21, 2020; Accepted – April 15, 2020
Available Online – April 25, 2020

DOI: http://dx.doi.org/10.18006/20.20.8694.2.185.192

ABSTRACT

Responses of drought tolerant (DT) and drought susceptible (DS) Ethiopian groundnut varieties to terminal drought stress were compared to determine the traits behind drought tolerance. Drought (D) induced from 91 to 105 days after sowing (DAS) reduced leaf RWC (relative water content, %), leaf area (cm² plant⁻¹), Chl (chlorophyll, mg g⁻¹ fresh weight), RDM (root dry mass, g plant⁻¹), ADM (above-ground dry mass, g plant⁻¹), TDM (total dry mass, g plant⁻¹) and plant height (cm); however, D increased SLM (specific leaf mass, g m⁻²). High leaf RWC in DS types reinstated the hypothesis that capacity to save leaf water is not a method of drought tolerance. Although there were insignificant Chl differences between DT and DS types, dry matter accumulation (RDM and ADM) was higher in DT types, which is attributed to higher SLM in DT types. SLM had significant positive relationship with RDM. An increase in plant height without increase in leaf area explains drought susceptibility in DS types. Resumption of irrigation on 106 DAS resulted in an increase in leaf RWC; however, this accompanied no resurrection response in terms of studied physiological and growth parameters and thus, it was not possible to restore pod yield after D impaired groundnut growth. Certain parameters were higher in DT types, positively correlated with DRI (drought response index) and primarily decided by the genotype; such parameters were concluded to be the traits behind drought tolerance.

KEYWORDS

Drought susceptibility
Drought tolerance
Peanut
Specific leaf mass
Water stress

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Peer review under responsibility of Journal of Experimental Biology and Agricultural Sciences.

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Groundnut responses to terminal drought stress

1 Introduction

Groundnut (Arachis hypogaea L.) is a significant crop plant utilized to produce foodstuff and cooking oil. Being a rain-fed crop (Nagaveni & Khan, 2019), it generally undergoes D under field conditions that brings about reductions in crop yield. Besides, D is a predisposing factor for aflatoxin production in groundnut (Waliyar et al., 2003). D is a devastating physical stress and more challenging to the attempts of breeders (Tuberosa & Salvi, 2006). Breeding drought tolerance in groundnuts cultivars would reduce yield losses due to D in rain-fed growing areas (Kakeeto et al., 2020). Breeding works to develop drought tolerance have been hampered in the past by its quantitative genetic base and by low understanding of the physiological base of productivity under D (Passioura, 2002). Hence, improvement of the current knowledge of reactions of crops to D and the methods contained in drought tolerance have turn out to be main goals of research and investment, with the crucial objective of producing crops with better WUE and reduced yield loss due to D (Somerville & Briscoe, 2001; Zhang et al., 2004).

Plants notice and react quickly to little changes in water status through a series of physiological, cellular, and molecular events (Chaves et al., 2009). D can activate a range of plant reactions, which comprise reduction in leaf RWC and water potential (Lawlor & Cornic, 2002), decrease in stomatal aperture and net photosynthetic rate. Photosynthesis is an important metabolism which is altered by D via reduced diffusion of CO₂ to chloroplast and metabolic limitations (Pinheiro & Chaves, 2011). Important assessments on crop reactions at large (Yordanov et al., 2000), and groundnut especially (Reddy et al., 2003), to D give additional knowledge on physiological features accompanying D. Nevertheless, there is even now no complete standard system for assessing drought tolerance, particularly since the physiological method is not all the time sufficient for selection on account of negative relationships between physiological attributes contained in drought adaptation (Turner et al., 2001). As a result, crop development plans have been unable to completely use current physiological data.

Responses of model plants namely, Arabidopsis and Craterostigma to D have been broadly studied (Yamaguchi-Shinozaki et al., 1995; Shinozaki & Yamaguchi-Shinozaki, 1996). Evaluation of the regulatory mechanisms of carbon assimilation in peanut due to forthcoming alterations in climate, including D, is inadequate (Clifford et al., 2000). Even though remarkable developments have been achieved regarding the type of actions happening in crops exposed to D, explanation of the metabolic regulation is even now absent (Rolland et al., 2006; Shinozaki & Yamaguchi-Shinozaki, 2007). Jeyaramraja & Thushara (2013) postulated a series of physiological reactions in peanut exposed to D. However, holistic studies in groundnut on the relationships among physiological, growth and yield parameters and their changes due to terminal D under natural field conditions are limited. As groundnut is mostly grown as rain-fed crop, it faces D during terminal stages of crop growth (Hampannavar & Khan, 2019), which results in reductions in yield and quality. Hence, it is essential to produce crops that bear D. Knowledge of drought tolerance mechanisms in legumes innately adjusted to D, such as groundnut, is essential in identifying markers for drought tolerance which in turn, can aid in plant breeding programmes. Nevertheless, little literature is available in groundnut on the physiological and growth parameters especially during the terminal stages of crop growth which is prone to D under field conditions i.e., from 90 to 110 DAS. Hence, the present study has been taken up.

Bacharou Falke et al. (2019) stated that investigation of groundnut genotypes response to drought stress could contribute to improving drought tolerance and productivity. Hence, in the present investigation, responses of DT and DS groundnut varieties during terminal stages of growth (90 to 110 DAS) was studied. This study was planned to investigate the consequence of D on certain physiological and growth parameters in Ethiopian groundnut varieties differing in drought tolerance, because it is assumed to be helpful in identifying traits behind tolerance/susceptibility to D.

2 Materials and Methods

The experiment was conducted inside “Natural Beauty Initiative Centre”, Main Campus, Arba Minch University, Ethiopia during April to September 2014.

2.1 Plant Material

Pods of six groundnut varieties were collected from Werer Agricultural Research Centre during April 2014. Pod and seed characteristics of these varieties were published (Jeyaramraja & Fantahun, 2014). These varieties were categorized into DT (ROBA, Werer 962, NC-4x) and DS (FAYO, Tole 2, Werer 964) types based on DRI values (Table 4) obtained from two growing seasons (Jeyaramraja & Fantahun, 2016).

2.2 Experimental Design

The experimental design was Randomized Block Design (RBD) with three replications. There were 6 experimental plots for each variety (3 for C and 3 for D) and since totally 6 varieties were used in this study; there were totally 36 plots (18 for C and 18 for D). A buffer zone of 2 m was left between C and D plots to avoid diffusion of water through soil layers during D induction period from C to D plots.
2.3 Experimental Layout

After ploughing the field three times into a fine tilth, experimental layout was made. Each plot had 4 numbers of 5 m ridges. Distance between two adjacent ridges was 60 cm. Inter-row spacing between plants was 30 cm while intra-row spacing between plants was 10 cm. Each plot was surrounded by bunds. Each plot had a length of 5 m and width of 3 m. Hence, the size of one plot was 15 m². The size of total experimental layout was 600 m².

2.4 Cultivation practices of groundnut

The soil was loamy. Sowing was done manually on both sides of ridges at ~4 cm depth. Sound, mature and good quality kernels were only selected for sowing. Kernels were subjected to treatment with Mancozeb (4g kg⁻¹ kernels) to guard the juvenile seedlings from root-rot and collar-rot infection. Compost (2 t ha⁻¹) was applied as basal dressing and incorporated well into the soil. Carbaryl 10 per cent DP was applied in soil at the time of seeding against ants/earwigs/termites.

2.5 Induction of D under field conditions

When groundnut is grown under field conditions as rain-fed crop, it does not experience D at all developmental stages. Jogloy et al. (1996) reported that groundnut generally experiences D during pegging and pod development and then may have sufficient quantity of water. This would cause severe decrease in yield, and the degree of decrease would rely on groundnut varietals (Kambiranda et al., 2011). Hence in the present study, D was induced by withholding irrigation in the field 91 DAS for a period of 15 days, i.e., up to 105 DAS, so that, simulated D could mimic the effects of naturally occurring D in the field. Rainout shelter which can cover the whole D plots was kept ready from 91 DAS to 105 DAS, so that, in the event of rainfall, the D plots could be covered immediately.

2.6 Irrigation Schedule

On the day of sowing seeds and 1 DAS, the field was irrigated. Then, irrigation was usually given once a week (i.e., 8 DAS, 15 DAS, 22 DAS and so on) based on soil water measured at four places (2 in C plots; 2 in D plots) with the help of a tensiometer. When water potential of top soil reaches -0.25 to -0.50 bars, irrigation was provided. Irrigation was skipped if rainfall replenished soil water. For C plots, irrigation continued until a week before harvest maturity of each variety. For D plots, the irrigation was skipped two times i.e., at 92 DAS and 99 DAS to induce D. It has to be noted that there was no rainfall in the field from 91 DAS to 105 DAS i.e., during the D induction period and hence, rainout shelter was not used to protect the D plots from rain. From 106 DAS, water supply was resumed for D plots and was continued until a week before harvest maturity of each variety.

2.7 Physiological and growth parameters

From each variety that is under C (or) D conditions, one plant was chosen randomly from each plot for analysis of below-given parameters which were measured 5 times (i.e., 90 DAS, 95 DAS, 100 DAS, 105 DAS & 110 DAS).

2.7.1 Plant water status

RWC was measured in the third leaf from the top of the main shoot as said by Clavel et al. (2006) employing the equation: 
\[\text{RWC} = \left(\frac{\text{FM} - \text{DM}}{\text{TM} - \text{DM}}\right) \times 100,\]
where FM was fresh leaf mass, TM was turgid mass after 4-h rehydration of the leaf in distilled water at room temperature under dark conditions, and DM was dry mass after drying at 85°C for 24 h.

2.7.2 Pigment estimation

Chl was determined spectrophotometrically as per the method of Sadasivam & Manickam (1996) in the second leaf from the top of main shoot.

2.7.3 Growth parameters

RDM, ADM & TDM were determined in line with Clavel et al. (2005). Plants were cautiously isolated from the soil and the roots were cleaned with water. Afterwards, RDM and ADM were determined after drying at 80°C for 2 days. TDM is the sum of ADM and RDM. Leaf area was determined by a non-destructive method employing allometric model (Kathirvelan & Kalaiselvan, 2007). In the third leaf from the top of main shoot, SLM was obtained (Clavel et al., 2005), which is the ratio of leaf dry mass per unit leaf area. Plant height was determined with a ruler from the ground to top of the main axis.

2.8 Statistical analysis

Three factor ANOVA was carried out for the analysis of physiological and growth parameters wherein Factor A is varieties (6), Factor B is treatments (2 - C and D) and Factor C is DAS (5 – 90 DAS, 95 DAS, 100 DAS, 105 DAS and 110 DAS). Critical difference (CD) values were computed at 0.05 and 0.01 levels to find out whether statistically significant differences existed within varieties, treatments, and/ or DAS. Interactions between the factors were also studied. Correlation coefficients among various physiological and growth parameters were studied to find out relationships among them.

3 Results and Discussion

To compare the effects of C and D on moisture content of groundnut leaves, RWC was used in the present investigation because it is thought to be a helpful integrator of crop water balance than leaf water potential (Wright & Nageswara Rao, 1994). Significant
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Variations were found among the groundnut varieties in terms of studied physiological and growth parameters except leaf area plant\(^1\) and Chl (Table 1). The fact that DS types had high leaf RWC in this work is of interest. DT *Phaseolus vulgaris* frequently open their stomata under harsh D (Costa França et al., 2000). DS cultivar had at all times high RWC mainly up to 35 days of D on two-week-old groundnut seedlings (Clavel et al., 2005). Above quoted earlier works and the present study reconfirmed the hypothesis proposed by Jeyaramraja & Thushara (2013) that capacity to save water in groundnut leaf is not a method of drought tolerance. Vadez (2014) also said that water saving mechanisms should not be considered as mechanisms of drought tolerance.

Although leaf RWC was higher in DS types (Table 1), Chl was the same in both DT and DS types. Kicheva et al. (1994) stated that reduction in rate of photosynthesis could happen owing to reduction in Chl under harsh D. Hence, same contents of Chl observed in this work must lead to same rates of photosynthesis in DT and DS types and so, same rates of dry matter production. However, RDM and ADM were higher in DT types. The reason for higher dry matter production in DT types is attributed to higher SLM values in DT types. It is imperative to note here that the DT types had 1.23-fold more SLM as compared to DS types.

Like leaf RWC, plant height was also higher in DS types. Leaf RWC showed positive correlation with plant height irrespective of DAS (r = 0.38, p<0.05, n = 36). It must be noted here that leaf area did not vary between DT and DS types (Table 1); hence, just an increase in plant height without increase in leaf area would not help DS types to be productive, which thus resulted in insignificant correlation between these traits with r value of -0.067. Reduction in plant height with almost unchanged total biomass accumulation but with increased grain yield/harvest index was achieved in certain breeding experiments (Cattivelli et al., 1994; Sláfer et al., 1994).

Drought is significantly (p<0.01) reduced leaf RWC, leaf area plant\(^1\), Chl, RDM, ADM, TDM and plant height (Table 1). SLM was significantly (p<0.01) increased due to D. The RWC reduction in plants under D could be related with reduction in crop vigour (Lopez et al., 2002; Halder & Burrage, 2003). Stomatal regulation of water loss has been identified (Chaves, 1991) as an initial reaction for conditioning the leaf water status of field crops, but it rigorously reduces carbon uptake and biomass production and hence, there was reduction in RDM, ADM and TDM in the present study.

Although DS types had significantly high leaf RWC than DT types under C conditions, the leaf RWC of DT types was almost equal to that of DS types under D conditions (Table 1). As compared to C, D caused 4.8 % reduction in leaf RWC in DS types whereas in DT types, it caused only 3 % reduction. Both under C and D conditions, DT types had significantly higher RDM than DS types. Higher RDM values in DT types may be attributed to deeper root system for soil moisture capture which is a successful method of attaining reproductive success under D (Kirkegaard et al., 2007). High dry matter production in DT cultivars under field conditions is caused by more capability to keep up transpiration, which is aided by deep roots (Blum, 2009). In a study in groundnut profuse root system in the deep soil was related to better yield under D and it was deduced that greater, lengthy and denser roots at deep soil was accountable for more water absorption (Jongrungklang et al., 2012). Although insignificant difference was found between DT and DS types regarding ADM and TDM under C conditions, DT types maintained significantly higher ADM and TDM than DS types under D conditions. D caused just 9.6 % ADM reduction in DT types while in DS types, it caused a tremendous reduction of 19.7 % (Table 1).

Because the plants in C and D plots were approaching maturity and in addition, the plants in D plots suffer D from 91 DAS, leaf RWC was found to decline significantly and progressively from 90 to 105 DAS (Table 2). However, due to resumption of irrigation on 106 DAS, leaf RWC could significantly (p<0.05) increase on 110 DAS in D plots. Although significant decrease in leaf area plant\(^1\) was observed from 90 DAS, the decrease was irregular (Table 2). Besides, due to resumption of irrigation on 106 DAS, leaf area plant\(^1\) could not increase significantly on 110 DAS in D plots. Chl was also found to decrease significantly from 90 to 105 DAS; however, Chl could not increase significantly on 110 DAS in D plots. RDM, ADM and TDM were on the decreasing trend significantly from 90 to 105 DAS. No resurrection response was found on 110 DAS in terms of RDM, ADM and TDM in D plots. Although statistically insignificant, SLM was found to increase from 90 DAS. Plant height had increased significantly from 90 to 105 DAS and there was statistically insignificant increase in plant height on 110 DAS in D plots.

As D was induced from 91 DAS, there were no significant differences between C and D plots on 90 DAS with respect to the studied physiological and growth parameters (Table 2). Leaf RWC was found to decrease both in C and D plots as the DAS increased. Reduction of leaf RWC in C plots was since the groundnut varieties were approaching maturity while in D plots, the reduction in leaf RWC was due to both reasons namely, D and approaching maturity. It is imperative to note here that the reduction of leaf RWC in D plots was more pronounced than in C plots until 105 DAS. Due to resumption of irrigation on 106 DAS, the leaf RWC could significantly revive on 110 DAS in D plots. RDM, ADM and TDM did not change significantly in C plots as DAS increased; however, these parameters decreased significantly in D plots until 105 DAS. No resurrection response in terms of RDM, ADM and TDM was observed on 110 DAS in D plots due to resumption of irrigation on 106 DAS. Plant height significantly increased in C plots with an increase in DAS; however, in D plots, there was no such increase in plant height (Table 2).
Table 1: Effect of drought stress on physiological and growth parameters of certain Ethiopian groundnut varieties

| Variety | Leaf RWC (%) | Leaf area (cm² plant⁻¹) | Chl (mg g⁻¹ FW) | RDM (g plant⁻¹) | ADM (g plant⁻¹) | TDM (g plant⁻¹) | SLM (g m⁻²) | Plant height (cm) |
|---------|--------------|--------------------------|-----------------|-----------------|-----------------|-----------------|--------------|-----------------|
| C       | D            | C                        | D               | C               | D               | D               | C            | D               |
| ROBA    | 80.3         | 76.5                     | 229.9           | 218.3           | 2.57            | 2.52            | 3.22         | 3.22           |
|         | DAS          |                          |                 |                 |                 |                 |              |                 |
| Werer 962| 79.5         | 78.4                     | 223.9           | 210.9           | 2.75            | 2.56            | 3.48         | 3.26           |
| NC-4x   | 80.2         | 77.8                     | 208.2           | 219.4           | 2.67            | 2.46            | 3.43         | 3.18           |
| Mean (DT) | 80.0         | 77.6                     | 220.7           | 216.2           | 2.67            | 2.51            | 3.38         | 3.22           |

| Variety | Leaf RWC (%) | Leaf area (cm² plant⁻¹) | Chl (mg g⁻¹ FW) | RDM (g plant⁻¹) | ADM (g plant⁻¹) | TDM (g plant⁻¹) | SLM (g m⁻²) | Plant height (cm) |
|---------|--------------|--------------------------|-----------------|-----------------|-----------------|-----------------|--------------|-----------------|
| C       | D            | C                        | D               | C               | D               | D               | C            | D               |
| ROBA    | 80.3         | 76.5                     | 229.9           | 218.3           | 2.57            | 2.52            | 3.22         | 3.22           |
|         | DAS          |                          |                 |                 |                 |                 |              |                 |
| Werer 962| 79.5         | 78.4                     | 223.9           | 210.9           | 2.75            | 2.56            | 3.48         | 3.26           |
| NC-4x   | 80.2         | 77.8                     | 208.2           | 219.4           | 2.67            | 2.46            | 3.43         | 3.18           |
| Mean (DS) | 81.4         | 77.5                     | 223.5           | 218.7           | 2.60            | 2.41            | 3.18         | 2.96           |

**Statistical significance**

| CD 5 % | between varieties | NS | NS | 0.09 | 0.37 | 0.38 | 2.1 | 1.2 |
|--------|--------------------|-----|-----|------|------|------|-----|-----|
|        | between treatments | 0.42 | 11.6 | 0.08 | 0.05 | 0.21 | 0.22 | 1.2 | 0.7 |
|        | variety X treatment| 1.03 | NS | NS | 0.12 | 0.52 | 0.54 | NS | NS |

Values are irrespective of DAS ie., averages of five various days after sowing (90, 95, 100, 105 & 110 DAS).

Table 2: Effect of drought stress on physiological and growth parameters in groundnut at various days after sowing

| DAS   | Leaf RWC (%) | Leaf area (cm² plant⁻¹) | Chl (mg g⁻¹ FW) | RDM (g plant⁻¹) | ADM (g plant⁻¹) | TDM (g plant⁻¹) | SLM (g m⁻²) | Plant height (cm) |
|-------|--------------|--------------------------|-----------------|-----------------|-----------------|-----------------|--------------|-----------------|
|       | C            | D                        | C               | D               | C               | D               | C            | D               |
| 90 DAS| 82.2         | 81.9                     | 257.5           | 257.9           | 2.72            | 2.73            | 3.28         | 3.30           |
| 95 DAS| 81.8         | 79.2                     | 218.0           | 172.4           | 2.63            | 2.43            | 3.28         | 3.18           |
| 100 DAS| 80.5         | 76.6                     | 216.1           | 229.7           | 2.64            | 2.43            | 3.30         | 3.04           |
| 105 DAS| 80.0         | 73.9                     | 216.4           | 207.4           | 2.58            | 2.35            | 3.28         | 2.94           |
| 110 DAS| 79.2         | 76.0                     | 202.4           | 219.9           | 2.59            | 2.37            | 3.26         | 2.99           |

**Statistical significance**

| CD 5 % | between DAS | 0.67 | 18.3 | 0.12 | 0.08 | 0.33 | 0.35 | NS | 1.1 |
|--------|-------------|------|------|------|------|------|------|-----|-----|
|        | treatment X DAS | 0.94 | 25.9 | NS | 0.11 | 0.47 | 0.49 | NS | 1.6 |

Values are irrespective of varieties ie., averages of six varieties.

Proportion of variation due to stress treatments is more with regard to leaf RWC, leaf area plant⁻¹, Chl, RDM, ADM and TDM (Table 3). On the other hand, proportion of variation due to variety is more followed by stress treatments and DAS regarding SLM and plant height. SLM is not developmentally controlled; but environmentally (by D) and, genetically controlled. SLM is an index of mass and activity of the mesophyll under unit area of leaf (Jun & Imai, 1999). Hence, higher values of SLM in DT types observed in this work might lead to an increase in leaf thickness (mesophyll mass and activity) and thereby, an increase in photosynthetic activity and dry matter production. It is imperative to note here that SLM had strong positive relationship with RDM (r = 0.612, p<0.001, n=36) based on

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data irrespective of DAS. From the significant interactions between variety and stress treatments (Table 3), it can be inferred that there is genotype-specific D response in terms of leaf RWC, RDM, ADM, and TDM. From the significant interactions between variety and DAS, it can be concluded that each variety responds differently to various DAS in terms of ADM and TDM (due to differences in days to maturity). Significant interactions between stress treatments and DAS were also noted, which suggest that D has different effects at various DAS in terms of leaf RWC, leaf area plant\(^{-1}\), RDM, ADM, TDM and plant height. Low total transpiration to control water loss, chlorophyll content, and root length density revealed drought tolerance associated traits for pod production in groundnut, according to Bacharou Falke et al. (2019). Savita et al. (2019) reported that RWC at 75 DAS, SLM at 45 DAS and SPAD chlorophyll meter reading showed significant positive association with pod yield.

### Conclusions

DT types registered high RDM, ADM, TDM and SLM; nevertheless, these traits could not be the traits of drought tolerance because except SLM, traits like RDM, ADM and TDM had insignificant relationships with DRI values obtained in a previous study on the same groundnut varieties. However, SLM showed significant (p<0.01) positive relationship with DRI. In addition, only SLM is decided primarily by the genotype/variety and hence, it is genetically controlled. This strengthens the hypothesis that drought tolerance is conferred by a mixture of many different traits at the genetic level and hence, SLM must be a marker for drought tolerance in groundnut.

In addition, we found that the ratios of SLM/RWC, SLM/RDM, SLM/ADM, SLM/Plant height, ADM/RWC had significant positive relationships with DRI and so, these ratios can be used as traits to identify drought tolerant varieties of groundnut in plant breeding/improvement programmes. DS types had significantly higher leaf RWC and plant height that are insignificantly related to DRI with r values of -0.451 and -0.628 respectively. Since only plant height is primarily decided by the genotype/variety, it may be a marker for drought susceptibility.
Abbreviations

ADM – aboveground dry mass; C – control, irrigated plants; CD – critical difference; Chl – chlorophyll; D – drought; DAS – days after sowing; DRI – drought response index; DS – drought-susceptible; DT – drought-tolerant; RDM – root dry mass; RWC – leaf relative water content; SLM – specific leaf mass; TDM – total dry mass

Acknowledgements

Financial support for this whole study by Arba Minch University (GOV /AMU /TH14 /CNS /BIOL /01 /06) is gratefully acknowledged. The authors thank Werer Agricultural Research Centre for providing the groundnut seeds.

Conflict of interest

Both the authors declare that there is no conflict of interest.

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