



Hormones and Soluble Sugars Contents Comparison on Cucumber Cultivars with Different Inflorescence Growth Habit

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Authors' contributions

This work was carried out in collaboration among all authors. All authors read and approved the final manuscript.

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Abstract

In flowering plants, the arrangement of flowers on a stem becomes an inflorescence, and a huge variety of inflorescence architecture occurs in nature. Inflorescence architecture also affects crop yield. Cucumber (*Cucumis sativa* L) possesses two types of stem growth habits. One type is the indeterminate stem, in which the terminal bud continues the vegetative activity of shoot apical meristem (SAM) during most of the growing season; the second type is the determinate stem, in which the vegetative activity of SAM ceases when it becomes a terminal flower. This research is important as it contribute to crop production by clarifying how plant hormones and total soluble sugars influence the development of different inflorescence architectures in *Cucumis sativa*, Understanding the physiological differences between determinate and indeterminate growth habits can support the development of improved cucumber varieties with higher yields and better flowering patterns. The study also provides valuable insights into the complex regulation of the

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shoot apical meristem, a key process in plant developmental biology. The study was carried out at Nanjing agricultural university (cucumber laboratory) to investigate the variation of plant hormones and total soluble sugars on cucumber varieties with different inflorescence growth habit, two cucumber varieties (CUS82 and CUS226) with determinate and CCMC with indeterminate inflorescence were used. Shoot tips and stem samples were collected in three replicates at different stages, each replicate included 10 and 5 plants for the shoot tip and the stem sample respectively. Plant hormones (Gibberellic acid, Cytokinin, Indole Acetic Acid) and total soluble sugars contents were determined using enzyme-linked immunosorbent assay (ELISA) technique. All statistical analyses were performed using STATISTICA version 6.0 (Stat Soft Inc., USA, 2001) package and graphs were generated using Graph prism. In this study, we highlight recent findings on the variation of plant hormones and TSS on cucumber varieties with different inflorescence architecture. Results shows that plant hormones and total soluble sugars contents on both shoot tip and stem varies significantly between the cucumber varieties with different inflorescence at various stages of plant growth, however relationship between hormones and TSS with physiological and regulation mechanism of inflorescence growth habit is not well understood and therefore further research is needed to relate how hormones and TSS affect the genes or the pathways that regulate terminal flower formation.

Keywords: Cucumis sativus L; Determinate growth; Indeterminate growth; terminal flower; shoot apical meristem; plant hormones; total soluble sugars.

1. Introduction

1.1 Roles of Phytohormones on Plant Growth and Developments

Plants continuously generate new tissues and organs through the activity of populations of undifferentiated stem cells, referred to as meristems since plant meristems can modulate their activity, they provide the developmental flexibility that allows plants to adapt their development in reaction to the environment (Scheres, 2007; Vernoux et al., 2010) The hormone interactions have several mechanisms, which act at both levels of hormone response and biosynthesis in creating a delicate response network (Hadi et al., 2015; Weiss & Ori, 2007). The impact of gibberellins, cytokinin and, auxin (IAA) were considered as essential for plant growth and development process (De Bruyne et al., 2014; Depuydt and Hardtke, 2011). Plant hormones regulate all stages of growth and development from embryogenesis to senescence (Davies, 2013; Pop et al., 2011).

Gibberellins are plant growth hormones which promote cell division and regulate numerous physiological processes including seed germination, stem elongation, leaf, root and reproductive organs expansion (Achard et al., 2009; Colebrook et al., 2014; Schwechheimer and Willige, 2009). Several studies described the inhibition of gibberellin biosynthetic pathway by growth retardants in order to control crop production. Growth retardants were employed to reduce the shoot system, thereby lowering the risk of lodging in cereal crops, also used in making ornamental plants more compact with better canopy structure as well as improving the formation of reproductive structures in many other crops. (Liangjiu et al., 1990; Rademacher, 2016; Sridharan et al., 2009; Sridharan et al., 2015). Previously, its effects were reported in decreasing the stem length and also was involved in vascular formation. It is also utilized in boosting the growth of agronomic and horticultural crops (Kuai et al., 2015; Wang et al., 1986; Moon et al., 2003).

Cytokinin are produced in growing areas such as root tips and meristems and are known to promotes cell division. They travel through the xylem to their working destinations, such as leaves and stems. Cytokinins perform several functions performed in plants, including stimulation of growth and cell differentiation in stems and roots with auxins, promotion of growth and development of chloroplasts, and production of anti-aging effects on some plant parts and more importantly cytokinin provides a younger and healthier look to plants. Moreover, cytokinins are now known to exhibit a wide range of other physiological effects on a variety of plants and plant tissues. Most cytokinins occur as free purine bases, nucleosides or nucleotides and as t-RNA constituents. They can be divided into the different groups such as: isopentenyladenine (iP) and derivatives, zeatin (Z) and derivatives, dihydrozeatin (DHZ) and derivatives. The plant hormone auxin (Indole-3-acetic acid) plays an instrumental role in meristem biology. Indole-3-acetic acid (IAA) is the most common, naturally occurring, plant hormone of the auxin class. indole acetic acid (IAA) (Auxin) is a natural auxin which is produced by plants, bacteria and fungi. In plants, IAA is critical for plant growth and development. The phytohormone auxin (IAA) has been shown to play a central role in the regulation of leaf growth and

development by controlling leaf initiation, specification of growth axes, morphogenesis and marginal patterning (Saini et al., 2017; Shwartz et al., 2016).

The concentrations of endogenous auxins. Indole-3-acetic acid (IAA) is one of the main endogenous auxins, but it is relatively labile (Ludwig-Müller, 2000). Other endogenous auxins, such as indole-3-butyric acid (IBA), are more stable and travel more efficiently by polar transport (Frick & Strader, 2018). Polar transport down the stem is the main mechanism of in plants depend on their rates of biosynthesis, transport, conjugation, and catabolism (Kramer and Ackelsberg, 2015) transport of auxins that are synthesized in apical meristems (Ludwig-Müller, 2011; Pop et al., 2011; Woodward and Bartel, 2005). Auxins are now considered important regulators of, for example, embryo development, meristem organization, apical dominance, and lateral root formation (Davies, 2013; Figueiredo et al., 2016; Korasick et al., 2013; Pop et al., 2011a; Woodward and Bartel, 2005).

1.2 Roles of Total Soluble Sugar (TSS) on Plant Growth and Development

Total soluble sugar (TSS) content is not only the main photosynthate in higher plants, but also the main form of carbohydrate metabolism and temporary storage. Liu et al. (2011) indicated that the soluble sugar content plays a very important role in carbohydrate metabolism. (Wang et al., 2008) reported that the photosynthate exists as a form of water-soluble carbohydrate and its main components are soluble sugar, starch and cellulose. Soluble sugar levels have also been shown to affect other phase changes, such as the onset of senescence (Paul and Pellny, 2003). Endogenous leaf sugar levels tend to increase during senescence. Similarly, application of exogenous sugars stimulates the early stages of senescence. Leaf senescence is the last step in the life cycle of plants. During the process, materials used to build up leaves during vegetative growth are remobilized and transported into the developing organs (Smart, 1994; Smart et al., 1994; Williams and Leopold, 1989). Although senescence occurs in an age-dependent manner in many species (Guamét et al., 1991; Nam, 1997), its initiation and progression can be modulated by a variety of environmental factors such as temperature, mineral deficiency, and drought conditions, as well as by internal factors such as plant growth regulators.

Cucumber (*Cucumis sativus* L.) is an economically important vegetable crop and is widely cultivated in the world with a total harvest of more than two million hectares in 2016. It is the second largest of the Cucurbits family and globally ranking 4th in quantity of world vegetable production. *Cucumis sativa* L also possesses two types of stem growth habits. One type is the indeterminate stem, in which the terminal bud continues the vegetative activity of SAM during most of the growing season; the inflorescences of this type are axillary racemes (Liu et al., 2011). The second type is the determinate stem, in which the vegetative activity of SAM ceases when it becomes an inflorescence; this type has both axillary racemes and a terminal raceme.

The objective of this study was to investigate the variation of hormones and soluble sugar contents on shoot tip and stem of different cucumber (*Cucumis sativus* L.) varieties with different inflorescence growth habit. In this context, Knowledge on the level of their concentration on cucumber with different inflorescence growth may give insight to more research on whether they are involved in any ways either directly influencing the formation of terminal flower or indirectly by regulating physiological mechanism or the genes that triggers the formation of terminal flower in cucumber (*Cucumis sativus* L.).

2. Materials and Methods

2.1 Experimental Material

The experiment was carried out at Baima experimental farm of Nanjing Agricultural University, Jiangsu Province of China which is located at Latitude 32° 3' 4.96" N, and Longitude 118° 36' 38.78" W. Three cucumber varieties CUS82 and CUS226 both with determinate growth and CCMC with indeterminate growth were obtained from the cucumber laboratory gene bank and grown during 2019 spring and 2019 autumn seasons. The soil at the experimental site is a clay loam. The experimental design was a completely randomized block design.

For planting, seeds of the above named cucumber varieties were treated with hot water at between 50-55 °C for a period of 3-4 hrs. and then seeds were put at a temperature of 25-28 °C for pregermination to occur which took 1-2 days depending on the environmental temperature, the pregerminated seeds were transferred in to small

trays where they stayed for 3 weeks during spring season and two week during autumn season and then transplanted into the experimental greenhouses with drip irrigation and black polythene mulch. 60 replicates of each cultivar were transplanted using a complete block design of which 30 replicates of every cultivar were removed during every time of destruction sample collection.

2.2 Sample Collection for Hormones and Soluble Sugar Determination

Shoot tips and stem samples were collected at 3 and 4 different stages respectively. The different stages were designated as Stage 1 (when the plant has only one true leaf), stage 2 (three true leaves) stage 3 (flowering stage) and Stage 4 (terminal flower stage) only for the stem since at this time the determinate shoot tip was converted into flower and therefore no tip. Samples were collected in three replicates, each replicate for hormones included 15 and 10 plants for the shoot tip and the stem respectively. During sample collection the shoot apex at different mentioned stages were carefully expunged from 15 shoot tip per replicate and immediately put in liquid nitrogen, also about 3mm of the stem from 10 plants per replicate was cut and put in a 2ml tube and immediately put in a liquid nitrogen. All the sample were taken to the cucumber laboratory and kept in the negative 80 °C fridge until the time for hormones and soluble sugar determinations

2.3 Determination of Hormone and Total Soluble Sugar Contents

A total of 0.3 g (dry weight) of stems and shoot tips from at least 10 and 15 individual plants for stem and shoot tip respectively were used for measurements of soluble sugar and determination of hormone contents (Rosa et al., 2009). To quantify content of, GAs, CK and IAA contents, 0.2-g fresh tissues samples were prepared for phytohormone extractions, hormonal analysis and quantification were performed using the enzyme-linked immunosorbent assay (ELISA) technique. After thorough grinding in liquid nitrogen, the samples were extracted overnight with extracting solution at 4 °C in the dark. The homogenate was filtered and methanol fractions of the extracts were collected after centrifugation, passed through a Sep-Pak C₁₈ cartridge (Waters Ass., Milford, MA) and dried under N₂. The residues were dissolved in phosphate buffer. The ELISA for GA, CK and IAA was performed on a 96-well microtitration plate. After adding standard hormone, sample extracts and antibodies, the coated plates were incubated for 40 min at 37 °C. After rinsing four times, 100 µL peroxidase-labelled goat anti-rabbit immunoglobulin was added to each well and the plate was incubated for 40 min at 37 °C. Coloured substrate (phenylenediamine) was added to each well, and the reaction was halted by the addition of 3 M H₂SO₄. Absorbance at 490 nm was detected using an ELISA spectrophotometer and used to calculate, GA, CK and IAA contents (Weiler et al., 1981). Each sample was measured three times, with three replicates and each replicate was composed of 10 plant for stem samples and 15 plants for shoot tip sample.

2.4 Data Analysis

Data for endogenous hormone and soluble sugar contents are presented as mean ± SD for three replicates. 15 and 10 plants were considered as one replicate for shoot tip and stem respectively), a non-parametric Analysis of Variance (Kruskal Wallis test) was applied to calculate the significant differences between the comparisons (corrected $p \leq 0.05$). The parameters that contributed significantly to the final score were determined by Multiple comparisons of mean ranks. All statistical analyses were performed using STATISTICA version 6.0 (Stat Soft Inc., USA, 2001) package. Graphs were generated using Graph prism.

3. Results

The performance of cucumber plants with different growth habits is shown in Fig. 1. In indeterminate genotype (CCMC), the shoot apex growth developed continually, with the elongation of stem, and its inflorescence growing definitely (Fig. 1a, e). Also, result indicated that the shoot apex of CCMC had regular differentiation (Fig. 1c). On the other hand, determinate genotype (D226) produced a cluster of flower buds at an early stage about 25 days after planting (Fig. 1b). We also observed significantly higher number of floral primordia at the shoot apex in the section of D226 compared to CCMC (Fig. 1d). More so, as the development of the stem terminates, a cluster of flowers was formed at the shoot apex of D226.

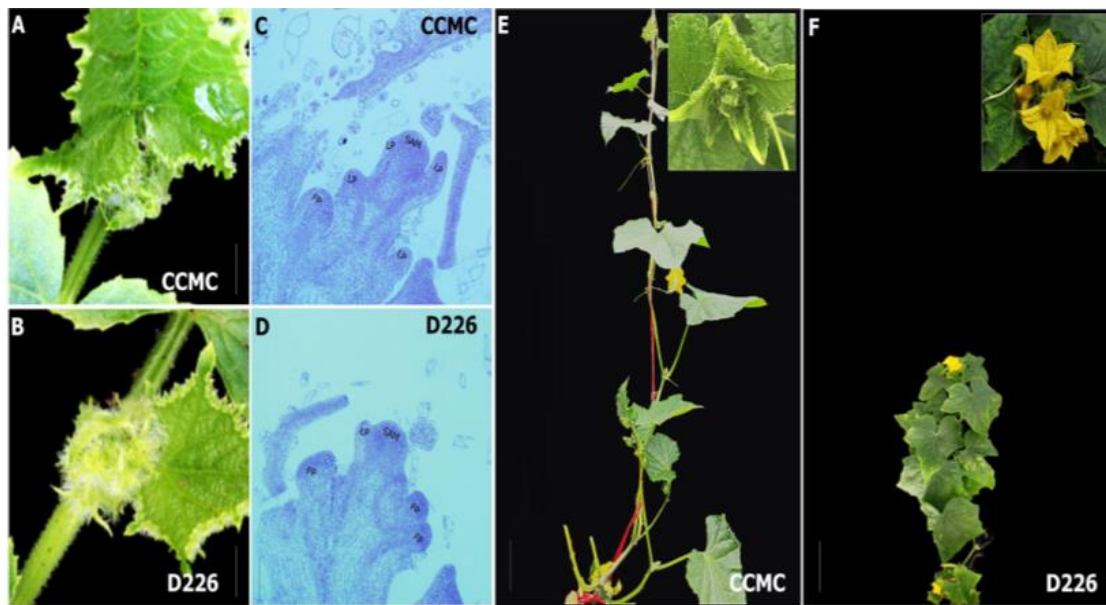


Fig. 1. Phenotypic differences in growth habit between cucumber varieties with indeterminate (CCMC) and determinate (D226) growth habit. a–d Show the changes at shoot apices of CCMC and D226, 25 days after planting. CCMC (e) maintained growth steadily, while D226 (f) already had terminal flowers at the same time of assessments

3.1 Comparisons of Gibberellin Contents on Shoot Tips and the Stem between Indeterminate (CCMC) and Determinate (CUS82 and CUS226) Cucumber (*Cucumis sativa*. L) Varieties

Gibberellins contents at the shoot tip differed significantly ($P < 0.001$) during all the tested stage of growth and it was significantly higher on determinate varieties compared to indeterminate variety, GA content of indeterminate variety remained the same during all the tested stages, similarly GA levels did not change significantly on determinate variety from stage one to stage two, however the level increased significantly during stage 3, Fig. 2. Also GA levels on the stem differed significantly ($P < 0.001$) between indeterminate and determinate varieties with determinate varieties having significantly ($P < 0.001$) higher GA content in the four stages compared to indeterminate variety, Fig. 3, and similar with the tip, the GA content on the stem were not significantly different among the different varieties from one stage to another, Fig. 3.

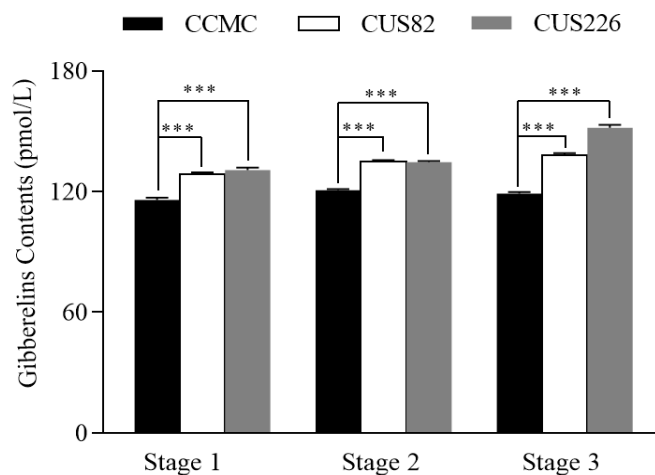


Fig. 2. Gibberellins contents at the shoot tips of different cucumber varieties with different inflorescence growth habit determined at different growth stages

Data are means of three replicates (\pm SD). Note: * Mean significant at 0.05 level ($P < 0.05$), ** Mean significant at 0.01 level ($P < 0.01$) and *** Mean significant at 0.001 level ($P < 0.001$)

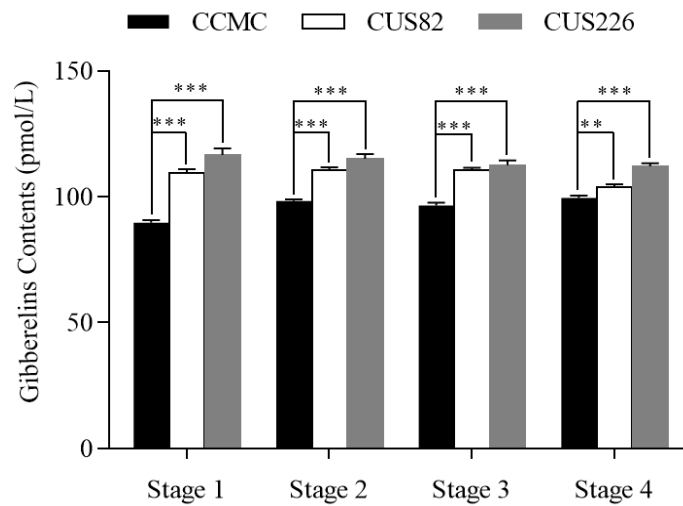


Fig. 3. Gibberellins contents on the stem of different cucumber varieties with different inflorescence growth habit determined at different growth stages

Data are means of three replicates (\pm SD). Note: * Mean significant at 0.05 level ($P < 0.05$), ** Mean significant at 0.01 level ($P < 0.01$) and *** Mean significant at 0.001 level ($P < 0.001$)

3.2 Comparisons of Cytokinins Contents on Shoot Tips and the Stem Between Indeterminate (CCMC) and Determinate (CUS82 and CUS226) Cucumber (*Cucumis sativa*. L) Varieties

Cytokinin levels on the shoot tip was significantly different at ($P < 0.001$) between the indeterminate and the two determinate varieties during the first stage of growth and at ($P < 0.01$) between CCMC and CUS82 during the second and the third stage, and significant at, ($P < 0.05$) levels between CCMC and CUS226 during the second and the third stage, Fig. 4. the level of CK for indeterminate variety increased significantly during all the three stages of plant growth. However, the CK levels did not change significantly on both determinate varieties during the three stages, Fig. 4. During the first stage the CK levels on shoot tip of indeterminate variety was significantly lower ($P < 0.001$) than that of both determinate varieties, however on stage 2 and 3, the GA levels of indeterminate cultivar increased and becomes significantly higher at ($P < 0.05$) and ($P < 0.01$) for CUS226 and CUS82 respectively, as the level of CK for determinate varieties did not change much from one stage to another, Fig. 4.

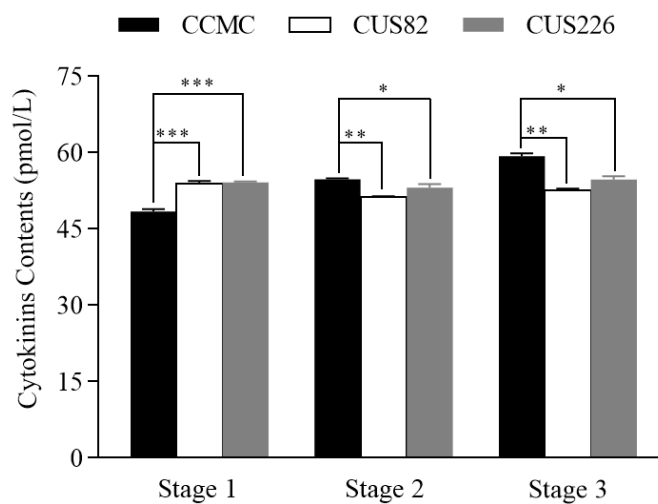


Fig. 4. Cytokinin contents at the shoot tips of different cucumber varieties with different inflorescence growth habit determined at different growth stages

Data are means of three replicates (\pm SD). Note: * Mean significant at 0.05 level ($P < 0.05$), ** Mean significant at 0.01 level ($P < 0.01$) and *** Mean significant at 0.001 level ($P < 0.001$)

Similarly, the CK levels on stem for indeterminate varieties increased significantly during all the three stages, though the CK levels for determinate varieties was significantly higher than that of indeterminate varieties during stage 1, 2 and 3 at ($P < 0.001$) Fig. 5. However, the ck level was not significantly different during stage 4 between CCMC and CUS82 and only significant at ($P < 0.01$) between CCMC and CUS226, Fig. 5. The CK levels on stem of determinate varieties increased slightly from stage one to stage 3 but decreased significantly during stage 4, Fig. 5.

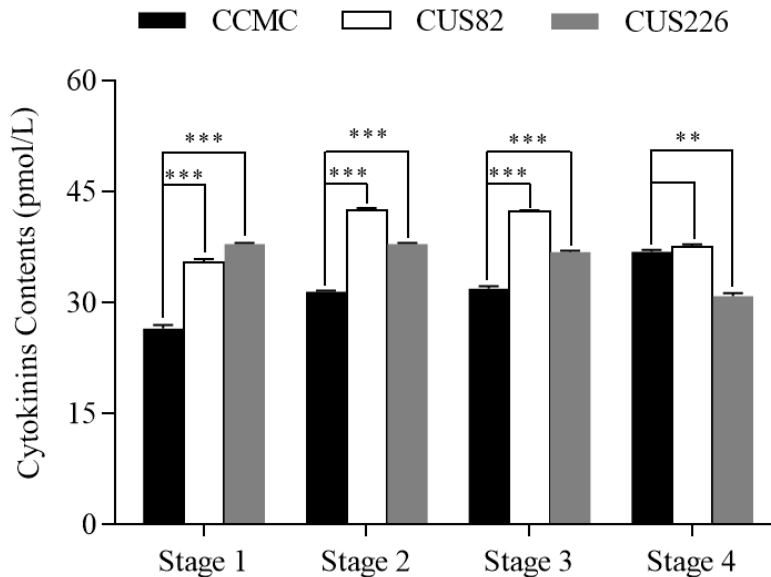


Fig. 5. Cytokinin contents on the stem of different cucumber varieties with different inflorescence growth habit determined at different growth stages

Data are means of three replicates (\pm SD). Note: * Mean significant at 0.05 level ($P < 0.05$), ** Mean significant at 0.01 level ($P < 0.01$) and *** Mean significant at 0.001 level ($P < 0.001$)

3.3 Comparisons of Indole Acetic Acid Content on Shoot Tips and the Stem Between Indeterminate (CCMC) and Determinate (CUS82 and CUS226) Cucumber (*Cucumis sativa* L.) Varieties

Indole Acetic Acid content on shoot tip was significantly different ($P < 0.001$) during the three tested stages of growth, the IAA levels were significantly higher on determinate varieties across all the three tested growth stages, Fig. 6. The IAA levels of indeterminate variety remained nearly the same and did not change significantly during three stages, however the IAA levels on determinate varieties increased significantly from stage one to stage two and did not change significantly during stage three. Fig. 6. Similarly, the IAA levels on the stem had significant difference between determinate and indeterminate varieties during all the stages of growth, at level ($P < 0.05$) during stage 1 and ($P < 0.001$) during stage 3 and 4, Figs. 6-7. Unlike on the shoot tips the IAA levels on the stem were significantly higher on the indeterminate variety compared to determinate varieties. IAA levels changed significantly among all the varieties from stage 1 to stage 2, however it did not change significantly from stage 2 to stage 3 and 4, Fig. 7.

3.4 Comparison of Total Soluble Sugars Content on Shoot Tips and the Stem between Indeterminate (CCMC) and Determinate (CUS82 and CUS226) Cucumber (*Cucumis sativa*. L) Varieties

The results of total soluble sugar comparison indicated that indeterminate variety (CCMC) had significantly lower levels ($P < 0.01$) of soluble sugars at the shoot tips compared to the two determinate varieties during the first stage of growth, Fig. 8, however the sugar levels for indeterminate variety increased significantly at ($P < 0.01$) and ($P < 0.001$) during stage two and three respectively and became significantly higher than those of determinate varieties which decreased from stage 1 to stage 3, Also notably the soluble sugar levels on determinate varieties were the same across all the stages, Fig. 8. On the stem the sugar levels were not

significantly different among all the varieties during stage one of plant growth, Fig. 8, also during stage 2, sugar levels were only significantly higher at ($P < 0.05$) between indeterminate CCMC and determinate CUS226, while its was not significantly different with CUS82. During stage 3 the sugar levels increased for determinate varieties increased significantly and became significantly higher at ($P < 0.001$) than in indeterminate variety, Fig. 9, however, during stage 4 the sugar levels on indeterminate variety continue to increase at the same time decreasing on both determinate varieties and therefore it was significantly higher ($P < 0.001$) on indeterminate variety compared to determinate varieties, Fig. 9.

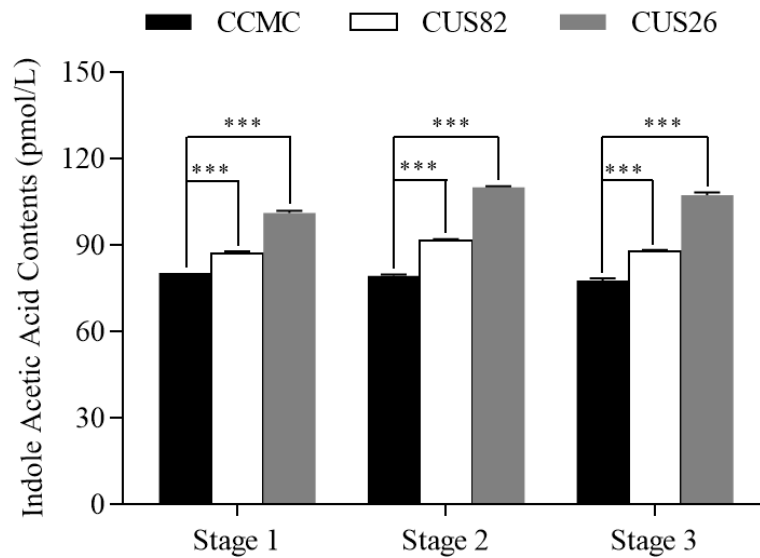


Fig. 6. Indole Acetic Acid contents at the shoot tips of different cucumber varieties with different inflorescence growth habit determined at different growth stages

Data are means of three replicates (\pm SD). Note: * Mean significant at 0.05 level ($P < 0.05$), ** Mean significant at 0.01 level ($P < 0.01$) and *** Mean significant at 0.001 level ($P < 0.001$)

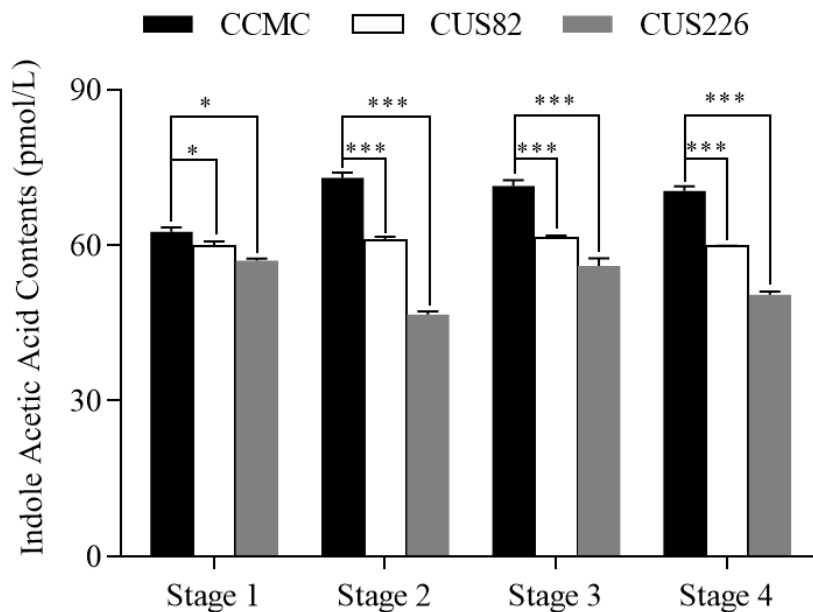


Fig. 7. Indole Acetic Acid contents on the stem of different cucumber varieties with different inflorescence growth habit determined at different growth stages

Data are means of three replicates (\pm SD). Note: * Mean significant at 0.05 level ($P < 0.05$), ** Mean significant at 0.01 level ($P < 0.01$) and *** Mean significant at 0.001 level ($P < 0.001$)

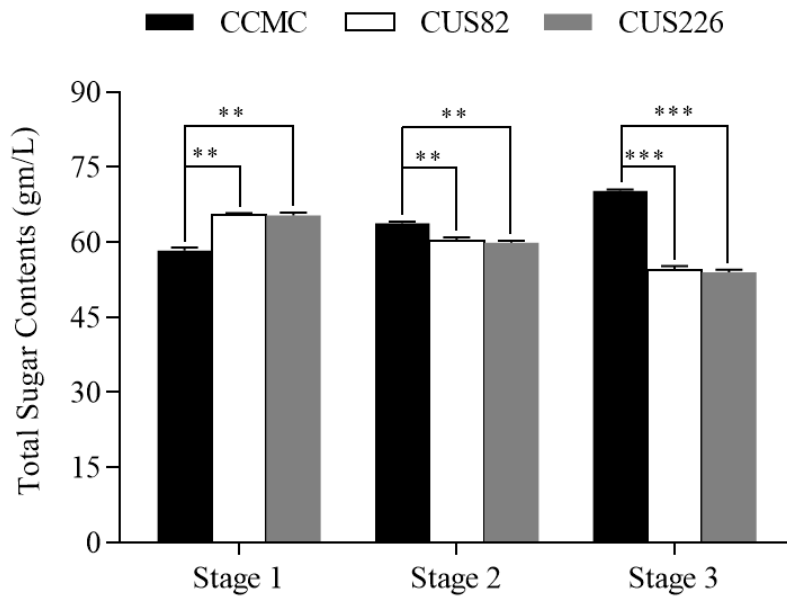


Fig. 8. Total soluble sugar contents at the shoot tips of different cucumber varieties with different inflorescence growth habit determined at different growth stages

Data are means of three replicates (\pm SD). Note: * Mean significant at 0.05 level ($P < 0.05$), ** Mean significant at 0.01 level ($P < 0.01$) and *** Mean significant at 0.001 level ($P < 0.001$)

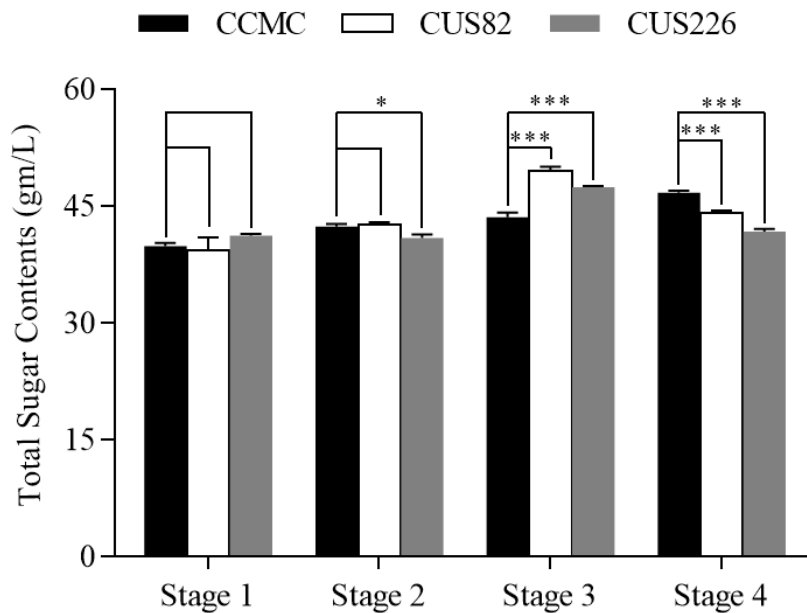


Fig. 9. Total soluble sugar contents on the stem of different cucumber varieties with different inflorescence growth habit determined at different growth stages

Data are means of three replicates (\pm SD). Note: * Mean significant at 0.05 level ($P < 0.05$), ** Mean significant at 0.01 level ($P < 0.01$) and *** Mean significant at 0.001 level ($P < 0.001$)

4. Discussion

4.1 Involvement of Pytohormones in Plant Inflorescence Architecture

The determinate/indeterminate growth habit is an important agronomical trait in the production of cucumber and many other vegetable crops. In cucumber production under protected environments, indeterminate growth habit

is ideal as it can be harvested throughout the production period hence leads to fruits sustainability and extend the growing season to maximize yield, while in certain production systems, like the once-over machine harvest system, determinate cucumber may be advantageous (Fazio et al., 2013).

Gibberellins (GAs) have been shown to affect flowering in a species-dependent manner: in long-day and biennial plants they have been shown to promote flowering, whereas in other plants, including fruit trees, they have shown to inhibit it. Recently GA pathway, which promotes flower induction has been identified in Arabidopsis. (Xu et al., 2022) discovered that gibberellin class of plant hormones are implicated in the control of flowering in several plant species. In Arabidopsis, severe reduction of endogenous gibberellins has been reported to delays flowering in long days and prevents flowering in short days, which is in agreement with our finding where we observed that an increase in GA level on the shoot tip of the determinate varieties during the production of terminal flower while the level on indeterminate variety remained significantly low, Fig. 3.

Exogenous application of GAs has been reported to accelerates flowering in wild-type Arabidopsis, particularly in short days (Langridge, 1957) and causal connection between endogenous GA levels and flowering in Arabidopsis has been confirmed with several GA biosynthesis and signaling mutants. However, this study is in contrast with other studies which reported that GA treatment during the flowering induction period reduces the number of flowers. Involvement of gibberellins (GAs) has been suggested in the regulation of floral induction in Mango, study done by (García-Pallas et al., 2001; Lenahan et al., 2006; Lord and Eckard, 1985) including mango (Tomer, 1984) reported that GA inhibits flower induction in many fruit tree, this result suggest that GA effect on cucumber is the same as that found on model plant Arabidopsis which may suggest that cucumber (*Cucumis sativa*. L) varieties and Arabidopsis share the same mechanism while this are in contrast with the influence of GA on fruit trees.

In this study we observed high content of GA on determinate varieties during the flowering stage which was in agreement with report by (Chen, 1987) who reported high GA activity during early flower bud. (Jutamanee, 1989; Tongumpai et al., 1991) found that GA concentration in the shoots increases before panicle emergence in some plants, which subsequently flower. These studies support our work which reported high concentration of GA on determinate varieties during flowering stages. These reports indicate that GA is involved in the regulation of floral induction in plant. Examination of the relationship between flowering and GA metabolism could provide evidence of GA involvement in floral induction in plants. However, the mechanism through which GA regulate flower formation need to be studies further at genetic level to unfold the genetic mechanism or pathway involved in this regulation.

In this study the level of Ck on the shoot tip was observed to differ significantly between the cucumber varieties with different inflorescence growth habit with determinate varieties having significantly ($P < 0.001$) lower levels of CK during terminal flowering stage than indeterminate variety. (Miyawaki et al., 2006) reported that increasing cytokinin concentrations and signaling activity increase meristem size and activity. Reduced meristem activity often leads to conversion of an IM into a terminal flower, which subsequently affects inflorescence architecture. Work in rice and in Arabidopsis showed that cytokinin levels affects meristem activity and inflorescence complexity. The current study agreed with a study done on *Arabidopsis* atipt3 5 7 triple mutants and atipt1 3 5 7 quadruple mutants which reported lower levels of cytokinin, leads to reduced IM size, and consequently the formation of a terminal flower, and conversion of an indeterminate inflorescence to a determinate inflorescence (Miyawaki et al., 2006).

Taken together, the results described above show that cytokinin may promote inflorescence complexity in different ways, by promoting meristem activity of IMs, and by promoting indeterminate lateral meristem formation in inflorescences that form terminal flower. Manipulating cytokinin levels directly or indirectly in crops is expected to change inflorescence complexity to increase yields (Ashikari et al., 2005; Kempin et al., 1995; Kurakawa et al., 2007; Li et al., 2013; Zhang et al., 2012).

The content of IAA was significantly high on the shoot tip of determinate compared to indeterminate varieties, on contrast the IAA content was much less on stem of determinate compared to indeterminate stem. The phytohormone auxin (IAA) has been shown to play a central role in the regulation of leaf growth and development by controlling leaf initiation, specification of growth axes, morphogenesis and marginal patterning (Saini et al., 2017; Shwartz et al., 2016). A key feature for auxin functions its differential distribution in precise locations within a specific spatiotemporal developmental context, resulting in the formation of auxin gradients

which are essential for plant growth and development (Koenig et al., 2009; Schwartz et al., 2016; Vanneste and Friml, 2009). Studies in *Arabidopsis* have demonstrated that local auxin activity gradient is generated by a cell-to-cell Polar Auxin Transport (PAT) system mediated predominantly by the auxin efflux carrier PIN-FORMED1 (PIN1), which transports auxin out of the cell in the direction of PIN localization (Friml et al., 2004; Michniewicz et al., 2007; Vanneste and Friml, 2009; Wiśniewska et al., 2006); whereas PIN1 polar localization in a particular plasma membrane domain is proposed to be mainly controlled through phosphorylation/dephosphorylation by the Ser/Thr protein kinase PINOID (PID) (Friml et al., 2004).

4.2 Involvement of Total Soluble Sugars in Plant Inflorescence Architecture

Plant carbohydrate status has been suggested to play a dominant role in flower bud formation in many crops (Monselise and Goldschmidt, 1982). For example, in mango, carbohydrate level has been reported to be associated with the intensity of flower induction (Chacko and Ananthanarayanan, 1982; Pongsomboon et al., 1997; Suryanarayana, 1978) but there is no reliable evidence of the role of carbohydrates in floral induction. In *Arabidopsis*, starch acts as a major integrator of plant growth (Nakagawa et al., 2012) and sucrose acts as an important signal. (Hisamatsu and King, 2008; Phavaphutanon et al., 2000), reported that high carbohydrate reserves within the shoots may be necessary for off-season flowering caused by paclobutrazol in mango. Their reports suggest that both endogenous GA and carbohydrate levels are related to the floral induction process affected flowering in plants.

Total soluble sugar (TSS) content is not only the main photosynthate in higher plants, but also the main form of carbohydrate metabolism and temporary storage. In this study we observed that the level of soluble sugars increase from stage one onward for indeterminate cultivar but in determinate type it decreases during the production of terminal flower, (Liu et al., 2011) indicated that the soluble sugar content plays a very important role in carbohydrate metabolism and has a close relationship with photosynthesis and production, this may explain the reduction of sugars during terminal flowering as more energy is required for production and many leaves are not photosynthetically active at this stage however on determinate type the sugar content continues to increase as the level of soluble sugar content was a sign of the supply ability of leaves and reflected transformation and ability of stem and shoot tips to use assimilates this was in agreement by a study done by (Kumudini et al., 2001). Wang reported that the photosynthate exists as a form of water-soluble carbohydrate and its main components are soluble sugar, starch and cellulose. Differences in water-soluble carbohydrates between cucumber cultivars with different growth habit was significant with indeterminate cultivar have more sugars on the shoot tip compared with indeterminate type. WSC in shoot tips increased throughout the growing season, while WSC contents in stems decreased during the terminal flowering stage. This decrease may indicate that soluble sugars as metabolically active carbohydrate is a factor involved during terminal flower formation. Soluble sugars help to ensure an adequate supply of building materials and energy to carry out specific developmental programs. For example, in-vivo and in-vitro experiments suggest that in some plant species, increasing sugar levels delay seed germination and stimulate the induction of flowering and senescence. In other words, it may be beneficial for plants to adjust the timing with which nutrient-intensive events occur to supply enough materials and energy for successful completion of those events. Levels of sugars, such as sucrose, have been postulated to affect the timing at which some plant species flower (Bernier et al., 1993), this was observed in determinate varieties where soluble sugars on stem increase sharply during stage 3 (flowering stage) and decrease during terminal flower formation stage. Soluble sugar levels have also been shown to affect other phase changes, such as the onset of senescence (Paul and Pellny, 2003). Endogenous leaf sugar levels tend to increase during senescence. Similarly, application of exogenous sugars stimulates the early stages of senescence. During the process, materials used to build up leaves during vegetative growth are remobilized and transported into the developing organs (Smart, 1994). Although senescence occurs in an age-dependent manner in many species (Noodén, 1988), its initiation and progression can be modulated by a variety of environmental factors such as temperature, mineral deficiency, and drought conditions, as well as by internal factors such as plant growth regulators (Uddin et al., 2008 and Wang et al., 2008) Since senescence can be induced by a large number of different conditions, and several signaling pathways are involved in the regulation of senescence, it is possible that environmental signals are integrated by sugar signaling. For example, experiments on sugar regulated senescence indicate that leaf senescence can be induced by growing *Arabidopsis* plants in the presence of 2% glucose in combination with low nitrogen supply (Pourtau et al., 2004; Wingler et al., 2004). Affymetrix Gene Chip data confirmed that changes in gene expression during glucose-induced senescence are characteristic of developmental senescence. Similarly, (Stessman et al., 2002) found that hexoses accumulate in senescing *Arabidopsis* leaves. However, the question remains as to what causes the strong accumulation of hexoses despite

the decline in photosynthetic carbon assimilation in senescing leaves. A possible source of hexoses is the breakdown of starch. In addition, (Jongebloed et al., 2004) showed that phloem blockage by callus deposition could lead to an age-dependent sugar accumulation.

5. Conclusion

In conclusion the study highlighted that cytokinin may promote inflorescence complexity in different ways, by promoting meristem activity of IMs, and by promoting indeterminate lateral meristem formation in inflorescences that form terminal flower. Also the phytohormone auxin (IAA) has been shown to play a central role in the regulation of leaf growth and development by controlling leaf initiation, specification of growth axes, morphogenesis and marginal patterning. Higher total soluble sugars in determinate plants during terminal flowering stage could indicate a higher capacity to store soluble sugars at this developmental stage, while the lower level observed in the indeterminate plants could indicate higher demands for cell division or elongation. This may also reflect the differences in the overall development of the inflorescence in the two different types of inflorescence growth.

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Author(s) hereby declare that NO generative AI technologies such as Large Language Models (ChatGPT, COPILOT, etc.) and text-to-image generators have been used during the writing or editing of this manuscript.

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Competing Interests

Authors have declared that they have no known competing financial interests OR non-financial interests OR personal relationships that could have appeared to influence the work reported in this paper.

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