FLOWER BUD DIFFERENTIATION IN PEPPER (*Piper nigrum* L.)

By

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THESIS

Submitted in partial fulfilment of the requirements for the degree of

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Faculty of Agriculture
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COLLEGE OF HORTICULTURE
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DECLARATION

I, hereby declare that this thesis entitled "Flower bud differentiation in pepper (*Piper nigrum* L.)" is a bonafide record of research work done by me during the course of research work and the thesis has not previously formed the basis for the award to me of any degree, diploma, associateship, fellowship or other similar title of any other University or Society.

Nalini

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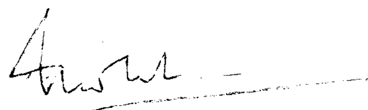

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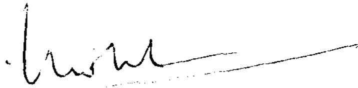

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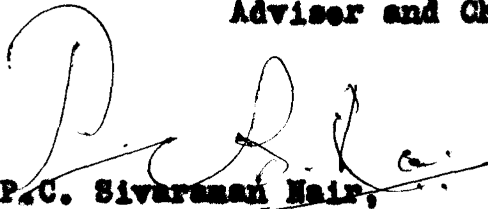

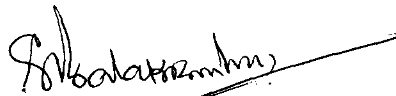

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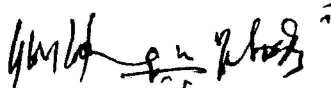

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Introduction

1. INTRODUCTION

For obtaining sustained higher yields in any perennial crop, the various cultural practices will have to be timed in relation to the cycle of flower bud differentiation. It is known that flower buds may be differentiated a few days to several months prior to the bud burst. With precise information on the site and time of flower bud differentiation, the application of fertilisers can be timed to help in the build up of carbohydrate and nitrogen reserves as well as favourable C/N ratio. By withholding irrigation at the appropriate time, the physiological maturity of fruiting branches/shoots can be brought about. The nature and quantity of vegetative portion to be removed by way of pruning can be decided only with the understanding of the site and time of flower bud differentiation and on the basis of an estimate of the expected crop. In short, precise information on the various aspects of flower bud differentiation will aid in the scientific management of any crop, including perennials.

Such information has been put to effective use in grapes. The time and extent of pruning; the frequency and quantum of irrigation water to be applied; the time, method and quantity of fertilisers to be applied, and even the

plant protection measures to be adopted have been standardised in grapes taking into consideration the site and time of flower bud differentiation. Anticliff and Webster (1955) devised a method of forecasting the potential crop in Sultana grapes, based on their studies on fruit bud differentiation. Possibility of refining the cultural practices in relation to flower bud differentiation exists in pepper also, which bears the crop in the leaf axils of the current season's growth on the laterals. Chandy and Pillai (1979) as well as Kurian (1982) have recorded evidences to indicate the ability of pepper to respond to pruning. Information on the factors influencing flowering/flower bud differentiation and on the various aspects of the differentiation _per se_, is essential before the results obtained in such studies can be exploited commercially.

Studies were undertaken at the College of Horticulture, Vellanikkara during 1981-82 to collect information on the factors influencing flowering/flower bud differentiation in pepper and on the chronological development of the vegetative and floral buds. The study being the first of its kind in pepper, there was need to standardise the microtechnique also.

Review of Literature

2. REVIEW OF LITERATURE

Pepper bears at the leaf axils of the current season's growth arising from the laterals. Chandy and Pillai (1979) reported that the production of laterals could be encouraged by judicious pruning. Before standardising the pruning schedule, it is essential to know exactly when and where the flower bud differentiation takes place. In the absence of studies on flower bud differentiation in pepper, the literature available on the subject in other perennial crops has been reviewed.

2.1. Factors influencing flowering/flower bud differentiation

2.1.1. Vegetative growth in relation to flower bud differentiation

The relationship between vegetative growth and flower bud initiation have been studied in various crops. According to Bernard and Thomas (1933), cessation of shoot growth was an important factor that brought about flower bud initiation in grapes. Shantha (1965) reported that the rapidity of the rate of growth of shoots discouraged initiation of flower buds in grapes. Chadha and Cheema (1971) observed that the mean shoot extension remained suppressed during the peak period of differentiation.

In mango, Singh and Khan (1939), Sen and Mallik (1941), Naik and Rao (1942) and Singh (1959) found that early initiation and cessation of growth followed by a definite dormant period helped the shoots to attain proper physiological maturity, which was essential for fruit bud initiation in them.

Blossom bud differentiation in Citrus spp. took place at the initiation of growth in spring or upon the resumption of growth. Prolonged moderately dry periods which cause an extended check in the growth, favoured flower bud differentiation (Abbot, 1935).

In the case of apple, Harley and Masure (1941) found that the time of bud differentiation was determined primarily by the amount of growth made by the spur. In Jonathan variety of apple, flower bud differentiation started about four to five weeks after the termination of shoot growth (Gyuro, 1959; Raven, 1968). Flower bud differentiation in regular bearing apple varieties started immediately after the cessation of shoot growth and in irregular bearing and intermediate varieties, three to five weeks after the cessation of shoot growth (Fulga, 1965).

In peach, Stadler and Strydom (1967) reported that differentiation of floral parts started just before the termination of shoot extension growth. Huet (1973) reported

that on the long shoots, the major factor contributing to floral initiation appeared to be the pattern of growth and the relative growth rate of shoots.

In blueberry, there were no consistent relationship between the vegetative growth or the time of growth cessation and the time of flower bud initiation (Wilson and Adam, 1966).

In raspberry, Williams (1954) reported that flower bud initiation occurred after the cessation of shoot elongation.

Bal and Gupta (1956) reported vegetative growth to be inversely proportional to the production of flower buds in jasmine. Muthuswamy et al. (1973) obtained higher production of flower buds in the early pruned plants. This they attributed to the increased vegetative growth, following pruning, potentially capable of forming flower buds.

In pepper, Kurian (1982) examined the relationship between pruning of shoots and subsequent production of laterals. He observed two growth flushes, one in May and the other during October-November. The second flush was relatively smaller. Pruning of hanging shoots significantly increased the mean extension of growth, production of bearing shoots, number of spikes and yield in the ensuing season. His studies indicated that pruning on May, gave higher yields.

2.1.2. Carbohydrate and nitrogen reserves

The carbon/nitrogen balance factor of Kraus and Kraybill (1918) was conceived by many workers as a factor governing the vital functions of fruit bud initiation. In grapes, Shantha (1965) found that those axillary buds subtended by healthy, green and active leaves when entered into the phase of initiation in the period between the 45th and 60th day from pruning differentiated into fruit buds and this was attributed to the existence of optimum carbon/nitrogen balance of tissue at the time of initiation. Chadha and Cheema (1971) observed that starch accumulation favoured fruit bud differentiation in the grape variety Perlette. Both started in the basal portion of the shoot and continued to the terminal portion. Rao and Sathyanarayana (1978) also reported increased C/N ratio between 40 and 90 days after pruning, which coincided with the period of fruit bud differentiation. However, they found that the high C/N ratio recorded in the shoots on the 100th day after pruning was not associated with fruit bud formation.

Evidences to the contrary are also on record. Winkler et al. (1962), Chitkara et al. (1972) observed that C/N ratio of shoot portions has no bearing on the differentiation of buds located on them in Anab-e-Shahi. Similar conclusions were also drawn by Khajuria et al. (1970) in Gulabi cultivar.

In mango, Naik and Shaw (1937), Sen (1946), Mallik (1953), Singh (1960) and Sen *et al*. (1963) reported that in almost all varieties except Baramasia higher starch reserve, total carbohydrate and C/N ratio in the shoots favoured flower initiation. Studies on the nitrogenous constituents in the mango stem and leaves by Chacko (1968) showed that the total nitrogen content was higher in the stem and leaves just before flower bud initiation. General levels of carbohydrate and soluble nitrogen were much higher in the flowering shoots than in the nonflowering shoots (Singh, 1959; Sen *et al*., 1965).

In citrus, C/N ratio was highest in the September flush, intermediate in the June-July flush and lowest in the March flush. It increased with the age of the shoots and the increase was more pronounced in the winter months. The carbohydrate content of the nonbearing shoots was greater than that of the bearing shoots (Kar and Randhawa, 1968).

In apple, high percentage of starch alone was found to be associated with the initiation of flower primordia (Harley and Masure, 1941). There was no obvious relationship between nitrogen in the spurs and the initiation of flower buds in them (Shahulka, 1962).

In *Jasminum grandiflorum*, Subramanian and Shanmugavelu (1981) obtained significant positive correlation between

carbohydrate level and flower bud initiation, indicating the importance of carbohydrates in flower bud initiation.

2.1.3. Climatic factors in relation to flower bud differentiation

Temperature relations have been indicated as important in determining the pattern of bud development. In grapes, Perold (1927) reported that warm and dry conditions in the preceding season had greater influence on fruit bud initiation. Kolesnik (1953) reported poor fruit bud initiation under low temperature conditions. Baldwin (1964) established a positive correlation between the intensity of fruit bud initiation and temperature conditions. Nikov (1964) suggested that grape buds do not need low temperature conditions during their active growth period to trigger fruit initiation. Buttrose (1969) reported that the number of buds initiated was closely related to the temperature conditions during a three-week period in which the node subtending the bud changed the position from the apex to ten nodes below. Dimitrieva (1969) found close relationships between the percentage of fruiting shoots and temperature sum (r=0.84).

Marked drop in the night temperature and relative humidity appeared to favour fruit bud differentiation in mango (Ravishankar et al., 1979).

Apple flower buds were formed more readily during warm

dry weather than during cool weather (Gribanovskji, 1969). Suzuki and Tanno (1971) reported that the average minimum temperature in early March and the average maximum temperature in mid-April were closely correlated with the start of the bud break.

In low bush blueberry, Hall *et al*. (1970) found that the number of primordial meristems and the degree of development of floret primordia were enhanced by warmer conditions.

Neduraman (1977) observed significant positive correlation between heat unit requirement and formation of flower buds in jasmine.

In grapes, it was found that artificial shading depressed the fruitfulness of the central buds, and yields were reduced due to retarded development of flower primordia (May and Anticliff, 1964 and Dikan, 1976). Shading greatly reduced the flower bud differentiation in apple (Kraybill, 1923; Auchter, 1926; Jackson and Palmer, 1977), apricot (Jackson, 1969) and in peach (Kraybill, 1923).

In mango, Chacko and Randhawa (1971) reported that high rainfall had depressing effect on the flower bud differentiation. Heavy rains during the critical period of flower bud initiation, stimulated vegetative growth at the expense of fruit production.

2.1.4. Physiological factors in relation to flower bud differentiation

2.1.4.1. Nutrition

Judicious and timely fertilization has been reported to promote flower bud differentiation in several crops. Kolesnik (1953) stated that the application of phosphatic fertilisers in the preceding season increased the fruitfulness of the dormant buds of grapes. He also obtained more fruitful shoots by the application of an aqueous solution of nitrogen, phosphorus and potassium. Arutjunan (1964) and Isoda (1964) recorded increases in fruitfulness due to the application of phosphatic fertilisers. Havelka (1964) recorded an increase in fruitfulness by the long term appli cation of phosphatic fertilisers. May and Anticliff (1964) and Alleweldt (1964) observed more differentiation of fruit buds when nitrogen application was timed just after the cessation of shoot growth. Srinivasan and Muthukrishnan (1970) reported that early application of potassium (20 days after pruning) advanced the bud development and correspondingly increased the fertility of the basal buds.

Nitrogen application stimulated flower production in apple (Delap, 1967; Hill-Cottingham and Williams, 1967), cherry (White, 1968), apricot (Jackson, 1970) and sweet lime (Singh and Bakshi, 1964). In strawberry, phosphorus

stimulated flower bud differentiation when applied at the time of bud initiation (Hedzaeva, 1962).

Alexander and Woodham (1964) and Coombe (1964) noted increased fruitfulness in 'Sultana' by the application of zinc sulphate.

2.1.4.2. Crop load

Fruiting intensity in the preceding season is known to influence the vigour and productivity of the perennial plants during the succeeding season. In grapes, Thomas and Bernard (1938) reported that a normal crop was always associated with greater fruit bud initiation in the season during which maturity of current crop and formation of fruit buds for the subsequent crop took place concurrently. On the contrary, Antcliff (1965) observed that crop load of the preceding season had only minor effect on the fruit bud initiation.

Investigations carried out by Thimmaraju (1966) in some of the mango varieties showed that fruit load on the tree appeared to be the main factor governing fruit bud differentiation in the succeeding year.

2.1.4.3. Growth regulators

Exogenous application of gibberellic acid reduces the flower bud initiation in a wide range of fruit crops such as

grapes (Alleveldt, 1964; Weaver, 1960), mango (Kachru et al., 1971), citrus (Monselise and Halevy, 1964; Hirose, 1968; Nir et al., 1972), apple (Guttridge, 1962; Dennis and Edgerton, 1966) as well as pear, peach, cherry and apricot (Hull and Lewis, 1959; Bradley and Crane, 1960). Application of B_9, CCC and TIBA promoted flower bud formation in a number of crops. Tuckey et al. (1966), Hull (1966) and Coombe (1967) obtained increased flower bud formation in grapes with B_9. Similar results were obtained with CCC by Sugiura et al. (1976) and Okamoto et al. (1977). Cessation of shoot growth and rapid increase in flower bud differentiation were obtained in apple with Alar (Batjer et al., 1964; Greenhalgh and Edgerton, 1966; Gols, 1967; Looney et al., 1967; Vanbelle, 1967; Vinbrants, 1967; Dalbro, 1970; Dimitrovski, 1976), CCC (Luckwill, 1966; Luckwill and Child, 1966; Marcelle and Raskin, 1967; Zika, 1977) and TIBA (Bukovac, 1968).

In mango during the period of flower bud differentiation, high amounts of auxin like growth promoting substances (Chacko, 1968) and certain inhibitors similar to abscisic acid (Chacko, 1968; Dutt and Dhillion, 1981) were observed. The amount of cytokinin was also found to be higher during the period of fruit bud differentiation in mango (Agarwal et al., 1980; Dutt and Dhillion, 1981). High level of cytokinin was considered helpful for floral initiation in apple also (Luckwill and White, 1968).

2.2. Site and time of flower bud differentiation

Flower bud differentiation in grapes has been reported to take place during the period preceding the fruiting season (Bernard, 1932; Rajaram *et al.*, 1964 and Chadha and Cheema, 1971). Wide variations have been reported on the time of fruit bud differentiation, depending upon the variety, the location and the environmental factors (Bernard, 1932; Bernard and Thomas, 1933; Winkler and Shemsettin, 1937). Histological studies on grape buds by Goff (1899) revealed that the initiation process of cluster primordia took place during October, in California. In Thompson seedless grapes grown in California, Perold (1927) observed a gradual trend of fruit bud initiation from the middle of June to the beginning of July. Similar observations were made by Patridge (1929) in the variety Concord. In the State Michigan, Snyder (1933) observed fruit bud differentiation in June, in the variety Concord. Fruit bud initiation in Sultana was observed by November in Australia (Bernard 1932; Bernard and Thomas, 1933), by June in California (Winkler and Shemsettin, 1937) and from middle of May to end of July in U.S.S.R. (Titova-Molcanova, 1951). Shoemaker (1955) stated that fruit bud initiation in grapes occurred during mid-summer and continued in the newly forming buds throughout the growing season. Hughin (1958) reported that in the variety Alsatian, cluster primordia

initiated during mid June in the primary latent buds. The process was found to be completed by August. Constantine (1958) reported that flower bud initiation in grape began soon after the appearance of the 17th or 20th leaf and this character was reckoned as a biological method for determining the time of fruit bud initiation. Khalil (1961) observed the initiation of fruit bud by the end of May in the variety Merlot and by the beginning of June in the variety Barbera, under the conditions prevailing in Italy. Under South Indian conditions, Rajaram _et al_. (1964) found that in Anab-e-Shahi, flower bud differentiation took place in November, that is around the 60th day after first pruning. Nanaya _et al_. (1968) reported that in Pachadraksha, Black Prince and Kishmish, cluster primordia were evident 35 to 40 days after the bud burst, while they were evident after 25 days in Bangalore Blue. Chadha and Cheema (1971) reported that flower bud differentiation in grapes started by April 20th in North India and peak differentiation was reached by the first week of June. However, the development of the differentiated buds continued upto the end of September. Rao and Sathyanarayana (1978) observed that flower bud differentiation in Anab-e-Shahi occurred from the 40th day to 70th day after pruning. Bindra (1981) reported that Beauty Seedless differentiated floral primordia as early as 11th April, whereas in Banquabad differentiation occurred about a week later.

He observed that Perlette showed differentiation of floral primordia in the samples taken on 3rd April, while in Anab-e-Shahi it occurred in the samples taken on 9th May.

Bernard (1932) established that the cluster primordium was terminal in origin; but appeared lateral to the apex during the subsequent developmental stages of the primordial shoots. Schrader (1923) mentioned that the optimum yields for a 12-bud cane appeared at the fourth bud in the variety Concord. Colby and Vogele (1924) reported that the buds close to the base were dormant or produced fruitless canes. Patridge (1929) reported that the buds in the middle portion of the canes were more productive than those at the tip or base. According to Clark (1925), fewer bunch primordia were found in the basal portion of the canes than farther out. Schrader (1928) also reported that the basal portion of the canes were least fruitful. In Concord grapes, Manney and Plagge (1934) observed that the basal buds were unproductive because of their position and by their competition for food reserves. Naik (1949) held the view that the basal buds or nodes were usually sterile or produced only vegetative growth. According to Venkataratnam *et al*. (1952), in Anab-e-Shahi, the cluster primordia appeared in the fourth and fifth nodes only. Antcliff and Webster (1955) stated that fruitfulness was always low at the base of the Sultana canes. Rao (1955)

reported that the basal buds as well as those beyond a certain number in a cane of *vinifera* grapes generally remained unproductive. Gourley and Howlett (1957) reported that in Michigan, the buds near the tip and base of the canes were less fruitful than those in an intermediate position. Rao and Muthuswamy (1957) found that the basal buds on the past season's canes (of the variety Anab-e-Shahi) were fruitful. According to Khalil (1961), the most fertile portion of the shoot of the variety Barbera was from the seventh to the thirteenth node. In Merlot, the fertility increased from the base to the sixth or seventh node, then decreased upto the eleventh node and increased again towards the tip. Subbiah (1969) observed that the terminal buds of Anab-e-Shahi canes were more fruitful. Khajuria *et al*. (1970) as well as Daulta and Bakshi (1971) reported that the basal buds of the vines were unproductive and there was no sign of flower bud differentiation in them.

In citrus, differentiation occurs at the initiation of growth in the spring or upon the resumption of growth at any other season of the year subsequent to a period of environmental conditions favourable for the accumulation of food reserves (Abbot, 1935; Randhawa and Dinsa, 1947; Ahamad and Khan, 1951; Ayalon and Monselise, 1960; Randhawa and Chopra, 1963; Mishra and Yamdagni, 1968).

According to Abbot (1935), blossom bud differentiation in the sweet orange variety Pineapple was observed from January 20th, in Florida. The terminal buds differentiated earlier than the lateral buds. West and Bernard (1935) found that in Australia, flower bud differentiation occurred in the early spring in Washington Navel and Valencia. At Lyallpur, Randhawa and Dinsa (1947) observed that more flower buds were differentiated on the early flushes than on the late ones. Fugitha and Yagi (1956) reported that in Japan, blossom bud differentiation occurred by the middle of December in Washington Navel, by late January in Valencia and Fakuhara and by early February in New Summer. They found that blossom bud differentiation continued for about four months in Washington Navel. In North India, the time of flower bud differentiation has been reported to be the beginning of January in Blood Red and the end of January in Jaffa (Babu and Kaul, 1972).

According to Abbot (1935), blossom bud differentiation in Deccan grape fruit was observed by February 13th in Florida. Ahamad and Khan (1951) reported that in Punjab, flower bud differentiation in grape fruit took place along with the growth in the latter half of February. The terminal primordia differentiated when the shoot was about to emerge, while axillary flowers differentiated when the shoot was about one-fourth of an inch long. The active period of differentiation extended

over a fortnight. Mishra and Yamdagni (1968) observed flower bud differentiation in grape fruit by the end of January.

Milelia (1960) found that in mandarin, anatomical pre-differentiation of flower buds occurred towards the end of January and the true morphological differentiation during the first week of March.

In mango, wide variations have been reported on the time of fruit bud differentiation from year to year, place to place and variety to variety (Singh, 1958). The time of differentiation of the flower bud of mango is reported to be the month of October in Florida (Sturrock, 1934; Mustard and Lynch, 1946). Late season varieties showed differentiation until the first week of November (Sturrock, 1934). Reece et al. (1946) stated that the differentiation began within a very short period before the expansion of the terminal buds in December to February in the Haden variety of mango, in Florida. They further stated that the process continued throughout the period of bud expansion. In India, October and first half of November have been reported to be the time of flowerbud differentiation in mango under Bihar conditions (Sen and Mallik, 1941). In Punjab, this period has been found to be from the middle of August to the end of October (Musahib-ud-din, 1946). Under Saharanpur conditions, fruit bud differentiation

was observed in December (Singh, 1960). Savant (1969) observed that fruit bud differentiation at Vengurla started during the first fortnight of August; but under Poona conditions the commencement was delayed upto September.

Petrucci and Crane (1950) and Rane and Singh (1965) found that initiation and differentiation of flower buds in fig occurred throughout the growing season, which is from the beginning of April to the 15th of July. Breba figs were produced from the buds differentiated in the year previous to fruit maturity. Second crop figs, on the other hand, were produced either from the buds differentiated during the previous year or from the buds differentiated during the season in which the fruits mature. The buds at the extremities were least fruitful. The second to fourth nodal regions were the most fruitful area.

According to Shukla and Bajpai (1974), the critical period of fruit bud differentiation in litchi was December.

In Jaman, the third week of January was taken as the critical period of fruit bud differentiation (Mishra and Bajpai, 1973).

In Avocado, the time of flower bud differentiation was in late October or November. Differentiation started with the development of second proximal axes. Development into bloom was not interrupted by a dormant period (Reece, 1942).

In temperate fruits, flower bud differentiation has been studied by a number of workers. In apple flower bud differentiation began at the end of June and by November the carpels and the stamens were formed (Gyuro, 1959; Marrow, 1962; Neumann, 1962; Marrow and Ricci, 1963; Buban, 1967; Deidda and Pisanu, 1968; Raven, 1968; Golikova, 1969). The period of floral induction in apple appeared to last from November to late December and the stages of floral differentiation from late December to mid-March in Chili (Feucht and Arancibia, 1970).

In pear, the period of fruit bud differentiation was observed to be from mid-July to mid-October (Huet, 1973; Grinenko, 1977).

Ullah (1954) reported that in the C.O. Smith peach at Palampur, differentiation took place during the first three weeks of July, while in double flowering peaches at Lyallpur it occurred throughout August and September. Yoshimura (1962) observed the time of differentiation of peach flower buds to be September in Japan. Hassan (1968) reported that in Havel fruit growing region, the time of differentiation was from 29th June to 23rd August.

Brown (1952), Molnar (1960), Basso (1962), Kovacev (1966), Anikeev (1969) and Fedchenkova (1973) observed that flower bud differentiation in apricot started in July and completed by the end of September.

In case of cherry, the time of flower bud differentiation was found to be from the end of July to the beginning of August (Reichel, 1965).

In plum, flower bud differentiation started by about mid-July and finished by early to mid-September (Volkova, 1970; Mostolovista, 1972, 1977; Beech and Reeves, 1978).

In strawberry, Robertson (1955) reported that the flowers appearing from late April to about early June were derived from primordia formed during late summer or early autumn of the previous year. He found that the early strawberry varieties grown near Dundee began to form flower primordia in August. In India, third week of November was observed to be the critical period of differentiation (Pathak and Singh, 1977 and Sharma and Singh, 1980) and the whole process of differentiation was completed within 25 to 30 days. Guttridge (1952) reported wide variations in the time of differentiation in different localities. Capellini and Rosati (1970) observed that in Californian varieties flower bud differentiation occurred for a long time; but in Souvenir, differentiation occurred for only a short time and in an irregular manner.

In blueberry, Aalders and Hall (1964) reported that the reproductive tissues were differentiated around the middle of August. Georgiev and Topchiski (1972) reported

that flower bud initiation started in late July and continued upto late February. The male and female gametophytes developed by April.

Waldo (1933) stated that the red raspberry varieties Oregon, Culthpert and Lloyd George had all differentiated fruit buds by November. In Scotland, Mathers (1952) found that in the varieties Malling Landmark and Lloyd George, the flower buds were differentiated by the middle of September. Robertson (1957) and Wood and Robertson (1957) also recorded similar finding with respect to the varieties Malling Landmark and Lloyd George.

In black currant, August was observed to be the time of flower bud differentiation (Naar and Wareing, 1961). They found that flower primordia were laid down in the axillary buds of the current year's shoot. Elerk (1968) reported that flower buds of the variety Silver Geiter differentiated from the end of June to the beginning of July and that the petals were formed only after deep dormancy.

Subramanian and Shanmugavelu (1981) reported that flower bud differentiation in Jasminum grandiflorum took place during the second week of February, that is, 55 days after pruning. Flower buds were initiated 45 days after pruning.

2.3. Stages of flower bud differentiation

In Concord variety of grapes, Patridge (1929) found that the primordial meristematic apex of the primary bud commenced its process of growth characteristically by producing many pointed outgrowths of different sizes at definite intervals, differentiating into well defined organs of primordial trait such as protective scales and stipular scales before producing the primordia of generative organs. Bernard (1932) in his studies with Sultana grapes in Australia observed two buds developing in the axil of each leaf in a young shoot. But as they were enclosed in a common protective scale, they appeared to the eye as one bud. Upon growth extension, they separated and one gave rise to a short shoot. The other bud meanwhile had developed two accessory buds, one on each side. Winkler and Shemsettin (1937) observed the formation of bract primordium as the first indication of the formation of the cluster primordium. Chadha and Cheema (1971) described the process of initiation and development of inflorescence primordia in the variety Perlette. They found the formation of six lateral outgrowths of the apical meristem identified as primordial leaves. These primordial leaves developed alternatively on the sides of the axis of the developing buds. Axis further elongated and additional primordia appeared towards the distal end. Axillary buds

also appeared in the axils of basal primordial leaves. The distal primordia soon acquired different shapes aiding distinction between leaf and cluster primordia. The leaf primordia were pointed, where as cluster primordia were blunt and broad. The clustery nature of the latter primordia was evident after this stage. Appearance of a bract subtending each cluster primordium was the further indication of development of the cluster primordia. The cluster primordium produced numerous growing points. Chadha and Cheema (1971) further found that the cluster primordium consisted of a complex branching system and the elongation of cluster branches occurred gradually with continued rapid division. With the advancement of the season, the cluster primordia increased in size with numerous growing points.

Broadening and flattening of the apical meristem with two lateral protuberances on either side of the bud was taken as the indication of blossom bud differentiation in all species of Citrus (Abbot, 1935; Randhawa and Dinsa, 1947; Mishra and Yamadagni, 1968; Babu and Kaul, 1972).

In mango, four stages in the development of the fruit bud have been identified (Sen, 1943; Mustard and Lynch, 1946; Khan, 1960; Gunjate et al., 1977; Ravishankar et al., 1979). High meristematic activity marked by the production of broad conical protuberances in the axils of scales has been pointed

out as the first sign of fruit bud differentiation in mango. In the second stage, the buds became plump and conically protruded out of the scales. The main axis elongated and became multilobed due to the development of primary branches of the flower panicle. Some of the side protuberances also became multilobed due to the presence of the primordia of the secondary branches. In the third stage, the flower buds became conical, plump and emerged out of the scales. During the fourth stage, the scales started loosening indicating the bud break.

Work done by Mustard and Lynch (1946), Musahib-ud-din (1946), Singh (1958), Karandhikar (1960) and Savant (1969) in different varieties of mango, in India and Florida, pointed out that there was no period of dormancy between floral differentiation and inflorescence expansion. The floral organs developed in succession - calyx, corolla, stamens and carpel. As against the above observation, Singh (1958) reported that the primordia of petals, stamens and staminodes appeared alternating with one another and with the sepals almost simultaneously. Karandhikar (1960) and Gunjate et al. (1977) reported that the whole process of differentiation was completed within two to two and half months.

In fig, Rane and Singh (1965) identified five stages in the differentiation of flower buds. During the first

stage, the bud primordium appeared to be roundish, convex and was composed of meristematic scale primordia. The bud primordium initiated one more scale in the second stage. By the third stage, the bud primordium had produced many scales, and had also broadened and elongated. During the fourth stage, the apical surface started turning concave. In the fifth stage, the apex turned completely concave and was lined with the floral primordia.

In litchi, Shukla and Bajpai (1974) reported that the apex of vegetative shoot was dome shaped with a uniform curve. Later, flattening and broadening of the apex was observed with a rapid elevation on both sides of the growing point. They observed that blossom bud differentiation was a continuous process and panicles appeared in the same manner as in mango.

In temperate fruits such as apple, pear, peach, apricot and cherry, the initial stages in the formation of the flower primordia were found to be similar; but the later stages differed between the species depending upon whether they formed a superior ovary or an inferior one (Vitkovskji, 1969). In the case of vegetative buds of apple, the surface of the growing point had greater breadth with less degree of convexity. First evidence of flower bud differentiation was the rapid elevation of the surface of the growing point into

a narrow conical form (Gyuro, 1959; Marrow, 1962; Marrow and Rici, 1963).

In strawberry, flattening and broadening of the apex with an irregular outline of the growing point was observed prior to floral initiation. Differentiation of floral parts was found in acropetal succession (Pathak and Singh, 1977). Sharma and Singh (1980) observed four stages in the development of flower primordia in Pusa Early Dwarf strawberries. According to them, the undifferentiated primordium in stage I was conical and had a regular outline. The initiation process was found to be accompanied by broadening and flattening of the growing point at the apex. In stage II, elongation of the primordium occurred and new growing points appeared at the base. In stage III primordia of secondary and tertiary flowers appeared at the base, just below that of the primary flowers. Sepals and petals developed in the primary flowers at this stage. In stage IV, rudimentary stamens and pistils appeared in the primary flowers.

In blueberry, appearance of flattened apical meristem with numerous protuberances was observed to be the first sign of flower bud differentiation (Aalders and Hall, 1964).

In *Jasminum grandiflorum*, Subramanian and Shanmugavelu (1981) reported that the organo-genesis took place in acropetal

succession in the sequence of sepals, petals, stamens and ovary; but the corolla tube formation was completed only after the differentiation of the ovary. They observed that the vegetative bud was characterised by a pointed, elevated and elongated meristematic apex in the centre enclosed by two lateral leaves. During the transition phase, the central dome enclosed by the lateral protuberances was very much reduced and appeared concave with bulges.

2.4. Microtechnique

Different methods of killing and fixing, dehydration and infiltration have been suggested for processing plant materials for microtome sectioning. According to Johansen (1940), Formalin-Aceto-Alcohol (FAA) was the most widely used fixative. He stated that FAA could be used with almost all plant materials intended for anatomical or morphological studies. He also found that the plant materials could be left in FAA almost indefinitely without appreciable damage. Besides, there was no necessity of washing out the killing fluid, if the Tertiary Butyl Alcohol (TBA) method of dehydration was employed. Johansen (1940) and Sass (1951) reported that Chrome-Acetic formulas were unsatisfactory for the bulky and woody subjects because of poor penetrating ability.

Bernard (1932), Snyder (1933) used FAA for killing

grape buds. The same was used by Haltvick and Struckmeyer (1947) in red raspberry, Randhawa and Dinsa (1947) in citrus, Nasr and Wareing (1961) in black currant, Mishra and Yamdagni (1968) in citrus, Mishra and Bajpai (1973) in jaman, Gunjate et al. (1977) in mango, Pathak and Singh (1977) and Sharma and Singh (1980) in strawberry and Subramanian and Shanmugavelu (1981) in jasmine.

Chadha and Cheema (1971) used Carnoy's fluid fallowed by FAA for killing and fixing grape buds.

Aalders and Hall (1964) and Hall et al. (1970) suggested Craf III killing fluid for blueberry.

Among the dehydrating methods, the TBA method was found to be the most satisfactory one (Johansen, 1935). Unlike the other two butyl alcohols, the odour of TBA was agreeable (Sass, 1951). Formerly, ethyl alcohol was used widely for dehydration; but it was found to have shrinking and hardening action on the tissues (Johansen, 1940).

Aalders and Hall (1964) used TBA for dehydration of blueberry stem sections. The same was used by Gunjate et al. (1977) in mango, Pathak and Singh (1977) and Sharma and Singh (1980) in strawberry.

Johansen (1940) and Sass (1951) reported that Saffranin and Saffranin-combinations were the most important and

suitable stains for morphological and cytological studies. They also found that the above stained the lignified, cutinized, suberised and chitinised structures as well as the chromosomes, nucleoli and centrosomes. Johansen (1940) reported that Hematoxylin was selective for cellulose, pectin and fungus mycelium and that this had no effect on the cell walls and plastids.

Saffranin and Fast Green-combination gave best results in red raspberry (Haltwick and Strukmeyer, 1947), citrus (Randhawa and Dinsa, 1947), mango (Gunjate et al., 1977) and strawberry (Pathak and Singh, 1977; Sharma and Singh, 1980).

Bernard (1932) used a dilute solution of Acid Fuschin in 70% alcohol for grape material. Snyder (1933) used Fast Green dissolved in 95% alcohol while Winkler and Shemsettin (1937) used Delafield's Hematoxylin, with Saffranin as a counter stain.

Mishra and Yamdagni (1968) used Delafield's Hematoxylin for citrus and Hall et al. (1970) for blueberry. Subramanian and Shanmugavelu (1981) used Hematoxylin and Eosin stains for Jasmine.

Materials and Methods

3. MATERIALS AND METHODS

The investigations on the flower bud differentiation in pepper were carried out at the College of Horticulture, Vellanikkara during the 12-month period from July, 1981 to July, 1982. The Panniyur-1 vines used in the study were six years old and were under uniform cultural treatments (as per the package of practice recommendations of the Kerala Agricultural University).

3.1. FACTORS INFLUENCING FLOWERING/FLOWER BUD DIFFERENTIATION

3.1.1. Extension growth

Twenty, six year old standards of the cultivar Panniyur-1 were utilised for studying the relationship between growth of the laterals and flower bud differentiation. Twentyfive laterals of two types (those that bore the crop during the past season and those that did not) from the twenty standards were marked at random and tagged. The length of the laterals was measured in centimeters at fortnightly intervals starting from 1st December, 1981 till 15th July, 1982. From the figures so obtained, the fortnightly extension growth of the two types of laterals was worked out. The data on extension growth was examined for the possible role in flower bud differentiation.

3.1.2. Carbohydrate and nitrogen reserves

For studying the carbohydrate and nitrogen reserves in relation to flower bud differentiation, the new shoots were utilised in addition to the two types of laterals mentioned in section 3.1.1. Four standards were marked at random for this purpose. From each standard, six each of the three types of laterals were collected for chemical analysis at fortnightly intervals from 1st October, 1981 to 15th July, 1982. The samples were labelled, dried in an oven at 80°C for 48 hours and powdered using a grinder (Multiplex) to a fineness 14 mesh. The total soluble carbohydrates and nitrogen levels in the powdered material were estimated and correlated with flower bud differentiation.

Total soluble carbohydrates in the samples was determined colorimeterically as per the method suggested by Deiras (1961). Nitrogen in the samples was estimated by the colorimetric method as suggested by Snell and Snell (1967).

3.1.3. Climatic factors

From the data collected at the Meteorological observatory in the campus, fortnightly averages of mean temperature, humidity, rainfall and sunshine hours were computed. These parameters were examined for their possible role in flower bud differentiation.

3.1.4. Direct/indirect effects of the factors on flower bud differentiation

Apart from total soluble carbohydrates, nitrogen and C/N ratio, the climatic factors namely temperature, humidity, rainfall and sunshine hours are some of the factors that influence the differentiation of flower buds. Path coefficient analysis was done to assess the direct and indirect effects of these factors on the differentiation of flower buds in the new shoot and in the two types of laterals.

3.2. HISTOLOGICAL STUDIES

3.2.1. Selection of material

For studying the site and stages of flower bud differentiation, twenty standards of the cultivar Panniyur-I were selected. A number of laterals (those that bore the crop during the past season and those that did not) were tagged separately on each standard. From the tagged laterals, ten each per plant were collected at random at fortnightly intervals starting from 1st August, 1981 to 15th July, 1982. The specimens were collected during the morning hours. Nodal regions of these laterals were then separated into 6.0 mm long pieces, labelled, killed and fixed as described in the following section for further processing. The new buds emerging out of the two types of laterals were also collected,

along with a piece of stem portion, labelled, killed and fixed for further processing.

For obtaining information on the time taken for initiation to completion of the different stages of flower bud differentiation, ten buds were collected daily starting from 25.5.1982. These buds were processed and examined for the different stages.

3.2.2. Processing of the specimens

3.2.2.1. Killing and fixing

In order to select an appropriate killing and fixing fluid the following were tried:

Formalin-Aceto-Alcohol (FAA)

Ethyl alcohol	-	50 ml
Glacial acetic acid	-	5 ml
Formaldehyde (37-40%)	-	10 ml
Distilled water	-	35 ml

Chrome-acetic and Flemming types

Stock solution	Chrome-acetic type					Flemming type		
	I ml	II ml	III ml	IV ml	V ml	I ml	II ml	III ml
1% Chromic acid	30	50	50	70	97	25	50	75
1% Acetic acid	70	50	-	-	-	10	-	-
10% Acetic acid	-	-	10	20	-	-	10	-
Glacial acetic acid	-	-	-	-	3	-	-	5
2% Osmic acid	-	-	-	-	-	10	10	20
Distilled water	-	-	40	10	-	55	30	-

Navaschin and Bouin types

Stock solution	Nava-schin ml	Navashin types					Allen Bouin types			
		I ml	II ml	III ml	IV ml	V ml	Bouin ml	I ml	II ml	III ml
1% Chromic acid	75	20	20	30	40	50	-	50	50	25
1% Acetic acid	-	75	-	-	-	-	-	-	-	-
10% Acetic acid	-	-	10	20	30	35	-	20	-	40
Glacial Acetic acid	5	-	-	-	-	-	5	-	5	-
Formaldehyde (37-40%)	20	5	5	10	10	15	25	10	10	10
Picric acid saturated aqueous	-	-	-	-	-	-	75	20	35	25
Distilled water	-	-	65	40	20	-	-	-	-	-

Based on the rapidity of killing (to retain more features of the living cells) and the absence of shrinkage of cells (when the killing solution will have the same osmotic pressure as the living cells), FAA was selected for killing and fixing of the specimens collected.

The plant specimens were immersed in glass specimen tubes (1.5 cm x 7.0 cm). The tubes were then labelled, closed with tight fitting corks and stored under room temperature.

3.2.2.2. Dehydration

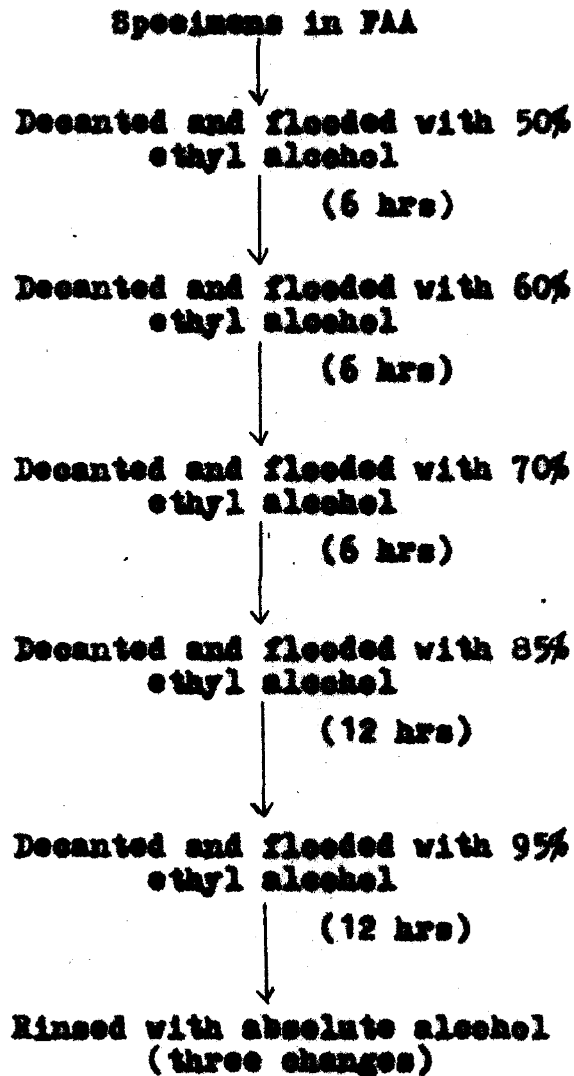
After one week of storing in FAA, the dehydration was started. Two methods of dehydration were tried.

Details of the methods followed are given below:

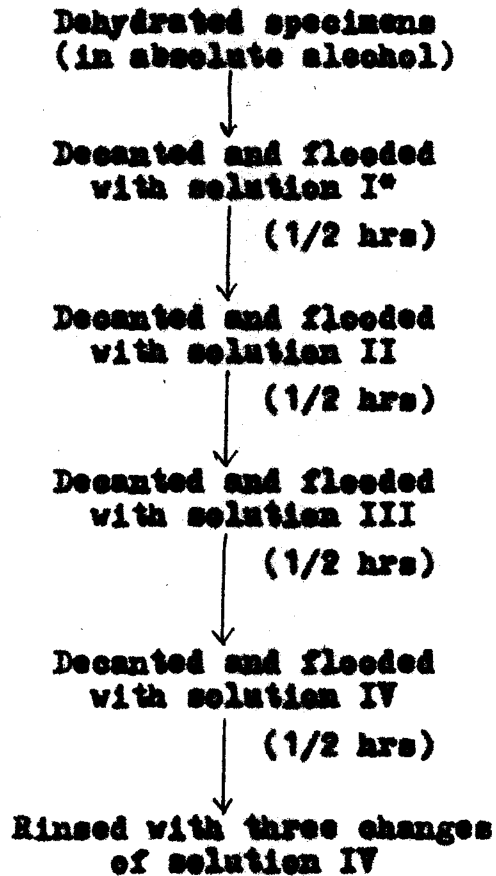
Dehydration by non-solvents of paraffin:-

A graded series of ethyl alcohol was used for dehydration. The materials were passed through the dehydrating series for four-, six-, and eight-hour durations. In all the schedules, the duration prescribed for the 85% and 95% alcohol treatments were double that of the first steps (for example, under four-hour schedule, eight hours were given for 85% and 95% alcohol treatment). Finally based on

the results obtained, the following series was selected:



The dehydrated specimens were then passed through a graded series of ethyl alcohol-xylene solution as indicated below:



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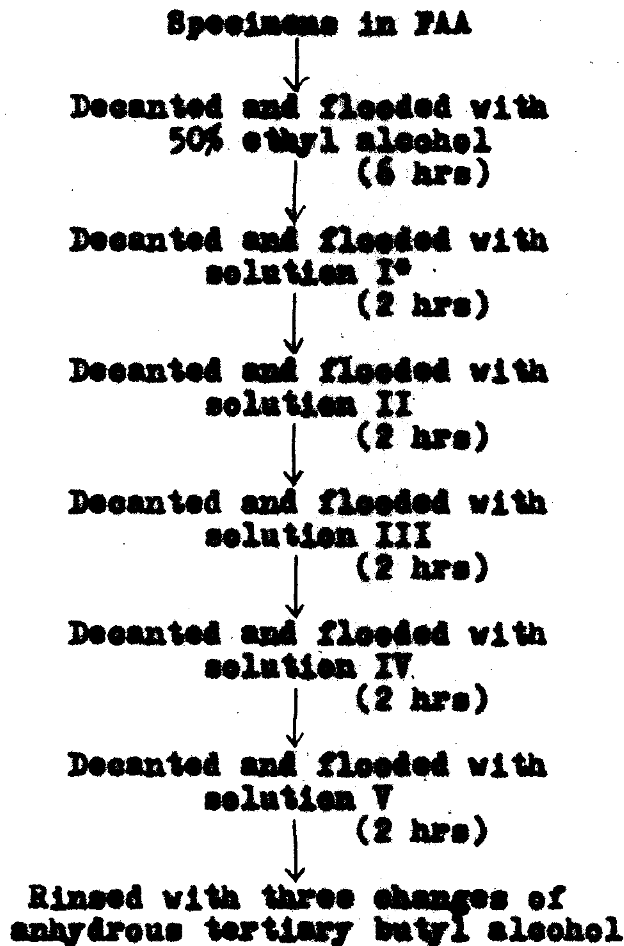
*

Grade number	Absolute ethyl alcohol (ml)	Xylene (ml)
Solution I	75	25
Solution II	50	50
Solution III	25	75
Solution IV	0	100

Dehydration by solvents of paraffin (Tertiary butyl alcohol method; Johansen, 1940):-

The specimens in FAA were passed through water-ethyl alcohol-tertiary butyl alcohol series for two-hour duration after treatment with ethyl alcohol for four, six and eight hours. Finally the following schedule was selected:



* Grade No.	95% ethyl alcohol (ml)	Absolute ethyl alcohol (ml)	Tertiary butyl alcohol (ml)	Water (ml)
Solution I	50	-	10	40
Solution II	50	-	20	30
Solution III	50	-	35	15
Solution IV	50	-	50	-
Solution V	-	25	75	-

Based on the degree of dehydration, firmness of tissues, absence of shrinkage of the protoplasm and absence of distortion of cells, the tertiary butyl alcohol method was ultimately selected for further work.

3.2.2.3. Paraffin infiltration

Immediately after the last stage of the dehydration series, infiltration was started. The anhydrous tertiary butyl alcohol was decanted and about 5.0 ml of fresh anhydrous tertiary butyl alcohol (just to cover the material) and a small quantity of chloroform (1/4 quantity of tertiary butyl alcohol) were added. To this, melted soft paraffin (m.p. 60-62°C) was added. The addition of paraffin was continued till a layer of undissolved wax remained on top of the solution. The specimen tubes were then corked and placed in an oven at 35°C for two days. After this period, the temperature of the oven was increased to 53°C for four hours. The specimen tubes were then taken out, one half of the solution decanted, an equal quantity of melted soft paraffin added and the tubes were replaced into the oven quickly. Four partial replacements were made as described above at intervals of four hours. The solution containing paraffin was then poured out and replaced completely with pure melted soft paraffin. After four hours at 60°C, another complete replacement was done to remove all the traces of the solvent.

3.2.2.4. Embedding

Embedding was tried by using soft paraffin (m.p. 60-62°C) and the mixture suggested by Hance (1933) without ceresin wax.

Based on the cutting property of the wax to form good ribbons of desired thickness, the mixture suggested by Hance (1933) was selected for embedding the specimens.

After paraffin infiltration, the specimens were flooded with the embedding mixture* and kept in an oven at 60°C for one hour. Embedding was done in boats made of 7.0 x 4.5 cm pieces of ivory paper (46 kg/144). The boats were first soaked in smoking hot wax and cooled. The embedding mixture containing the specimens were then poured into the boats. The specimens were arranged in a proper order with a heated needle before the solidification of wax. Space of one cm was given in between the neighbouring specimens. The identity of specimens were recorded. After hardening of the wax, the boat was placed in a vessel of cold water for cooling. The paper boat was then stripped out to give the paraffin blocks containing the specimens.

3.2.3. Microtome sectioning

The paraffin blocks were cut into pieces such that one piece contained one specimen. The edges of the pieces were

* The embedding mixture contains 100.0 g paraffin, 4.5 g rubber paraffin mixture and 1.0 g bee's wax.

trimmed to make the surfaces flat. The pieces were of approximately 1 cm x 1 cm x 1 cm. These pieces were then labelled properly and stored in small cardboard boxes at room temperature.

For microtome sectioning, the pieces were fastened to wooden mounting blocks. Hot paraffin was added to the top of each mounting block to form mounds and was allowed to solidify. The bottom of each embedded piece was then heated, pressed firmly on the top of separate mounting blocks and held in contact till the wax cooled down. A fillet of paraffin was also made around the embedded piece to provide a firm bracing. Excess paraffin was then removed and the sides of the blocks were levelled. Sections (10-14 μ thick) were then made using a Junior rotary microtome.

3.2.4. Affixing paraffin sections to the slides

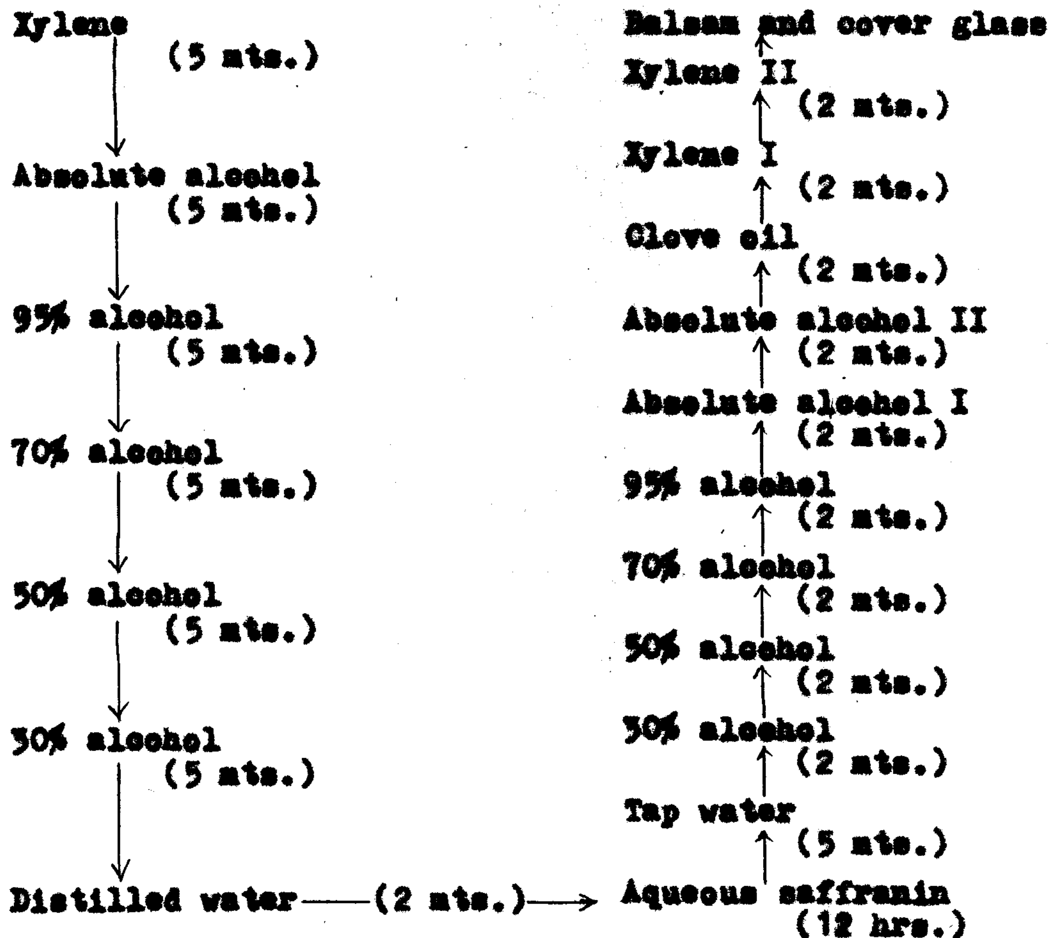
The sections were obtained in the form of ribbons. For fixing the ribbons to the slides, an adhesive was prepared by mixing equal quantities of egg white, glycerine and distilled water. A small drop of the above adhesive was placed on a clean slide and spread into a thin film. The slide was then flooded with water and a ribbon of sections placed on it. Excess water was drained. The slide was then warmed over a spirit lamp till the paraffin approached the melting point. While heating, the ribbon was kept floating

on the slide to permit expansion. The slides were then dried in an oven at 50°C for five hours. The details required for identification of the sections were marked on the slides.

3.2.5. Staining

Sections affixed to the slides were stained by immersion in specific reagents in staining jars. Saffranin and saffranin-fast green combination were tried. The staining chart for saffranin and saffranin-fast green combination are given below:

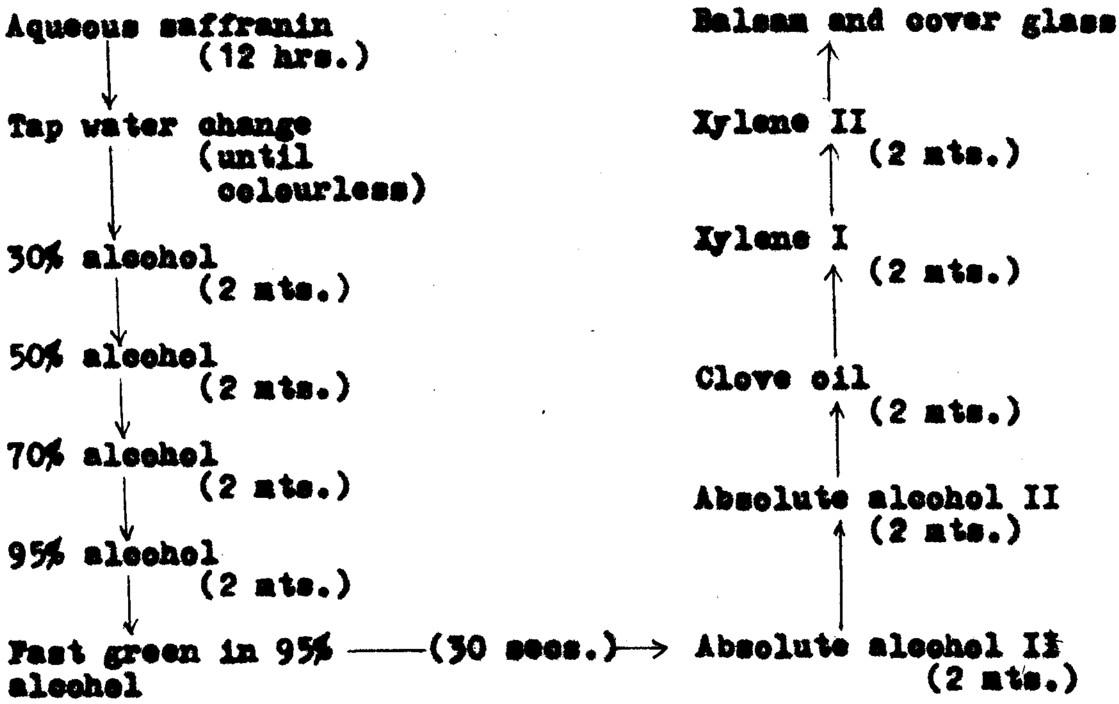
Staining chart for saffranin



Staining chart for saffranin-fast green

Pre-staining operations and intervals were the same as for saffranin staining.

Staining



3.2.6. Microscopic examination

The slides, after staining were observed through a binocular mono-objective microscope (Olympus KICBI) with 10 X objective and 10 X eye piece.

Critical examination was done using a high power objective with 40 X magnification. Measurements of the

selected sections were made using an occular micrometer, calibrated before use.

3.2.7. Photomicrography

Photomicrographs of the selected sections were taken using a pillar type 120 mm camera attached to a monocular mono-objective microscope (Olympus KICBI). ORWO black and white negative film of 120 ASA and Kodacolor negative film of 100 ASA were used for taking the photomicrographs.

Results

4. RESULTS

The results obtained in the investigations conducted on "flower bud differentiation in pepper" are presented in this chapter. The studies consisted of two parts, one on the factors influencing the flower bud differentiation and the other on the histological aspects of flower bud differentiation.

4.1. FACTORS INFLUENCING FLOWERING/FLOWER BUD DIFFERENTIATION

4.1.1. Extension growth

The data on the extension growth of the two types of laterals (those that bore the crop during the past season and those that did not) at fortnightly intervals from 1-12-81 to 15-7-82 are presented in Table 1.

Maximum mean growth was recorded during the fifteenth fortnight in both the types of laterals, 32.73 per cent of the total growth in the laterals that bore the crop during the past season and 31.04 per cent in the laterals that did not bear the crop during the past season. The months of June and July (fortnights XII to XV) contributed to 86.56 per cent of the total growth in the laterals that bore the crop during the past season and 82.52 per cent in the laterals that did not bear the crop during the past season. The first

Table 1.- Mean shoot extension growth in pepper (Piper nigrum L.)

Date of observation	Fortnight	Type of shoot: Those that bore the crop during the past season — Extension growth* (cm)	Percentage of the total	Type of shoot: Those that did not bear the crop during the past season — Extension growth* (cm)	Percentage of the total
1-12-81	Start of observation				
15.12.81	I	0.05	0.46	0.08	0.68
2.1.82	II	0.08	0.74	0.08	0.68
15.1.82	III	0.12	1.11	0.15	1.28
1.2.82	IV	0.11	1.01	0.11	0.94
15.2.82	V	0.05	0.46	0.005	0.04
2.3.82	VI	Nil	Nil	0.07	0.60
15.3.82	VII	Nil	Nil	0.06	0.51
1.4.82	VIII	0.07	0.65	0.10	0.86
16.4.82	IX	0.14	1.29	0.15	1.28
1.5.82	X	0.20	1.84	0.50	4.28
15.5.82	XI	0.65	5.99	0.74	6.33
1.6.82	XII	1.12	10.40	1.26	10.77
15.6.82	XIII	1.73	15.95	1.60	14.80
1.7.82	XIV	2.98	27.48	3.03	25.91
15.7.82	XV	3.55	32.73	3.63	31.04
Total		10.85	100.00	11.565	100.00

*Mean of 25 laterals randomly distributed over 20 standards

eight fortnights contributed only 5.72 per cent of the total growth in the laterals that bore the crop during the past season and 6.87 per cent in the laterals that did not bear the crop during the past season. Minimum growth was recorded during the fortnights V, VI and VII in both the types of laterals. From the eighth fortnight onwards, extension growth showed an increasing trend.

The relationship between the mean extension growth in the two types of laterals and the number of buds differentiating into flower buds in them has been depicted in Fig.5.

4.1.2. Carbohydrate and nitrogen reserves

Total soluble carbohydrates, nitrogen and C/N ratio of the two types of laterals (those that bore the crop during the past season and those that did not) and the new shoots are given in Table 2.

During the period of observation, total soluble carbohydrates varied from 1.91 to 7.90 per cent in the laterals that bore the crop during the past season, 1.82 to 6.60 per cent in the laterals that did not bear the crop during the past season and 2.97 to 7.26 per cent in the new shoots. Nitrogen content varied from 1.54 to 3.50 per cent in the laterals that bore the crop during the past season, 1.66 to 3.14 per cent in the laterals that did not bear the crop

during the past season and 1.77 to 3.72 per cent in the new shoots. C/N ratio ranged from 1.10 to 4.73 in the laterals that bore the crop during the past season, 0.83 to 3.79 in the laterals that did not bear the crop during the past season and 1.16 to 4.10 in the new shoots. Maximum content of total soluble carbohydrates was recorded during the second fortnight in the laterals that bore the crop during the past season, the sixteenth fortnight in the laterals that did not bear the crop during the past season and the nineth fortnight in the new shoots. Maximum nitrogen content was observed during the nineteenth fortnight in the laterals that bore the crop during the past season and in the laterals that did not bear the crop during the past season and the twentieth fortnight in the new shoots. Maximum C/N ratio was recorded during the second fortnight in the laterals that bore the crop during the past season, sixteenth fortnight in the laterals that did not bear the crop during the past season and the nineth fortnight in the new shoots.

4.1.3. Climatic factors

During the period of study, the average temperature varied from 25.40°C (August, 1981) to 31.30°C (March, 1982) and the relative humidity from 57.70 (February, 1982) to 91.15 per cent (June, 1982). The total rainfall during the period of study was 2568.30 mm. The monthly variation was

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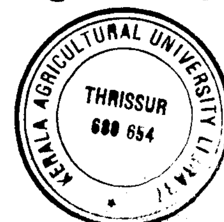
between 0 and 734.80 mm (June, 1982). The hours of sunshine ranged from 2.54 (July, 1982) to 10.00 (January, 1982).

A perusal of the data on the climatic parameters vis-a-vis flower bud differentiation (Fig.9) indicate that during June-July, when maximum number of buds in the two types of laterals differentiated into flower buds, the mean temperature, the mean rainfall and the mean relative humidity were high and the mean sunshine hours was the lowest.

4.1.4. Direct/indirect effects of the factors on flower bud differentiation

Path coefficient analysis was done to assess the direct and indirect effects of total soluble carbohydrates, nitrogen, C/N ratio, time factor and the weather parameters like temperature, humidity, rainfall and sunshine hours on flower bud differentiation in pepper. The results of the above analysis for the two types of laterals (that bore the crop during the past season and those that did not) and the new shoots are presented in Tables 3 to 5 and Fig. 1 to 3.

With regard to the laterals that bore the crop during the past season, the eight factors studied accounted for 98.17 per cent of the variation in flower bud differentiation (R^2=0.9817). Sunshine hours had the maximum direct effect (-0.52) on the rate of flower bud differentiation, even though it was negative. Time factor (0.34) and Nitrogen (0.23) had



positive effects; but were second to day length (Table 3, Fig.1). Humidity (-0.01) had the minimum direct effect. The indirect effects of all the factors through sunshine hours were high and it was more than its direct effect except for C/N ratio. Sunshine hours had the maximum correlation (r= -0.96) with flower bud differentiation, followed by rainfall (r=0.95) and time factor (r=0.87).

With regard to the laterals that did not bear the crop during the past season, the eight factors studied accounted for 96.68 per cent of the variation in flower bud differentiation (R^2=0.9668). Sunshine hours had the maximum direct effect (-0.44) and correlation (r= -0.95) with flower bud differentiation eventhough negative (Table 4, Fig.2). Time factor (0.42) and total soluble carbohydrates (0.33) had positive effects; but were second to day length. Temperature had the minimum direct effect (-0.02). The indirect effects of nitrogen, time factor, temperature and rainfall through sunshine hours were high and it was more than its direct effect except for time factor.

With regard to the new shoots, the eight factors studied contributed 99.62 per cent of the variation in flower bud differentiation (R^2=0.9962). Sunshine hours had the maximum direct effect (-0.40) on differentiation of flower buds (although negative), followed by nitrogen (0.37) and

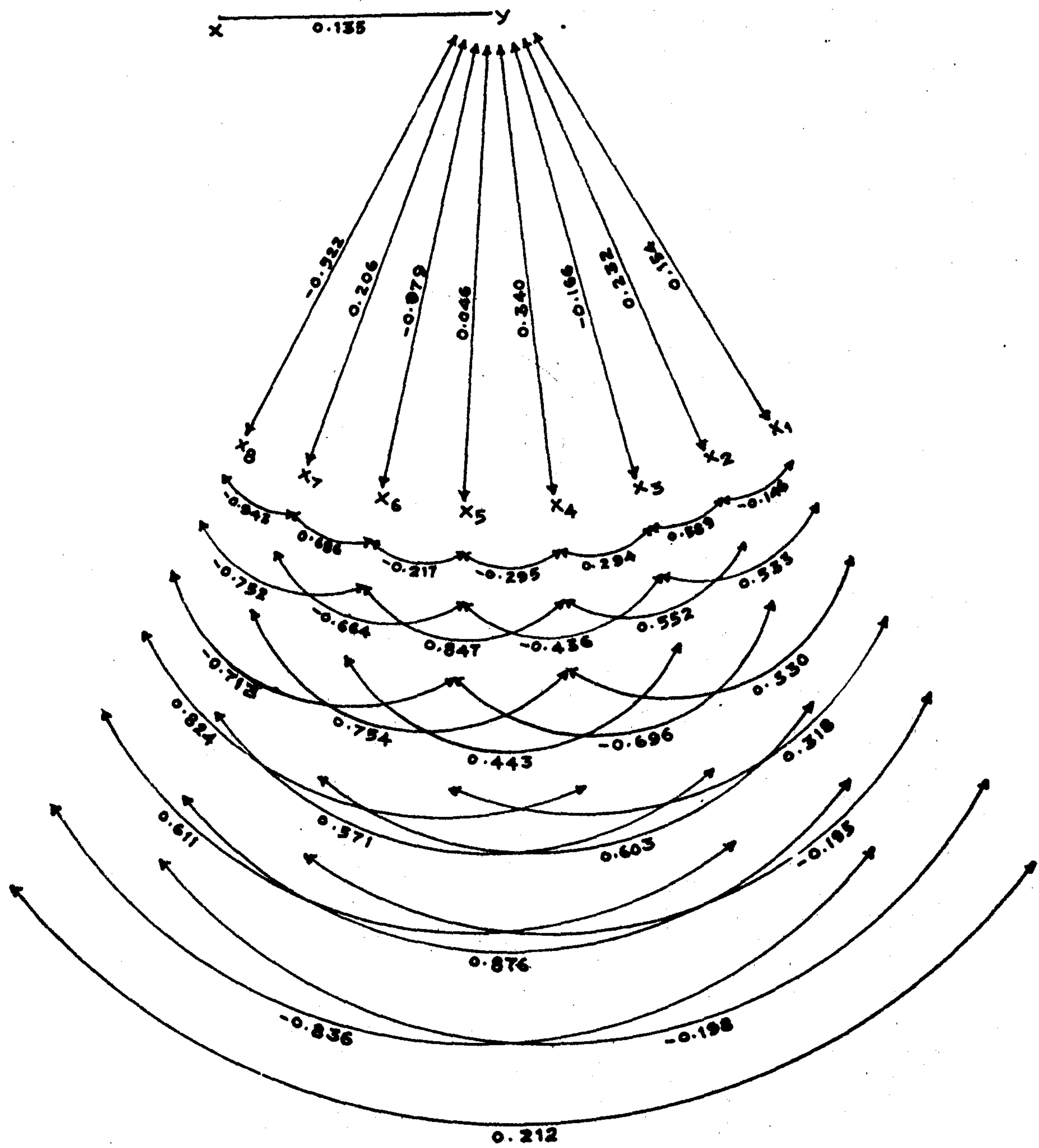
Table 3.- Path coefficients of various factors contributing to flower bud differentiation in pepper (Piper nigrum L.) (laterals that bore the crop during the past season)

Factors	Effect through								
	Total soluble carbohydrates	Nitrogen	C/N ratio	Time factor	Temperature	Humidity	Rainfall	Sunshine hours	Correlation with flower bud differentiation
Total soluble carbohydrates	-0.16	0.13	0.08	0.10	-0.02	-0.03	0.12	0.32	0.53
Nitrogen	-0.10	0.23	-0.02	0.19	-0.03	-0.04	0.18	0.49	0.83
C/N ratio	-0.09	-0.01	0.15	-0.11	0.01	0.05	-0.05	0.11	-0.20
Time factor	-0.05	0.13	-0.05	0.34	-0.01	-0.07	0.16	0.43	0.87
Temperature	0.07	-0.16	0.05	-0.10	0.05	0.02	-0.14	-0.37	-0.58
Humidity	-0.07	0.19	-0.03	0.29	-0.01	-0.01	-0.14	0.39	0.76
Rainfall	-0.09	0.20	-0.03	0.26	-0.03	-0.05	0.21	0.49	0.95
Sunshine hours	0.10	-0.19	-0.03	-0.28	0.03	0.06	-0.19	-0.52	-0.96

Underlined figures denote direct effects

Residual effects = 0.135

Fig.1- PATH DIAGRAM (LATERALS THAT BORE THE CROP DURING THE PAST SEASON)



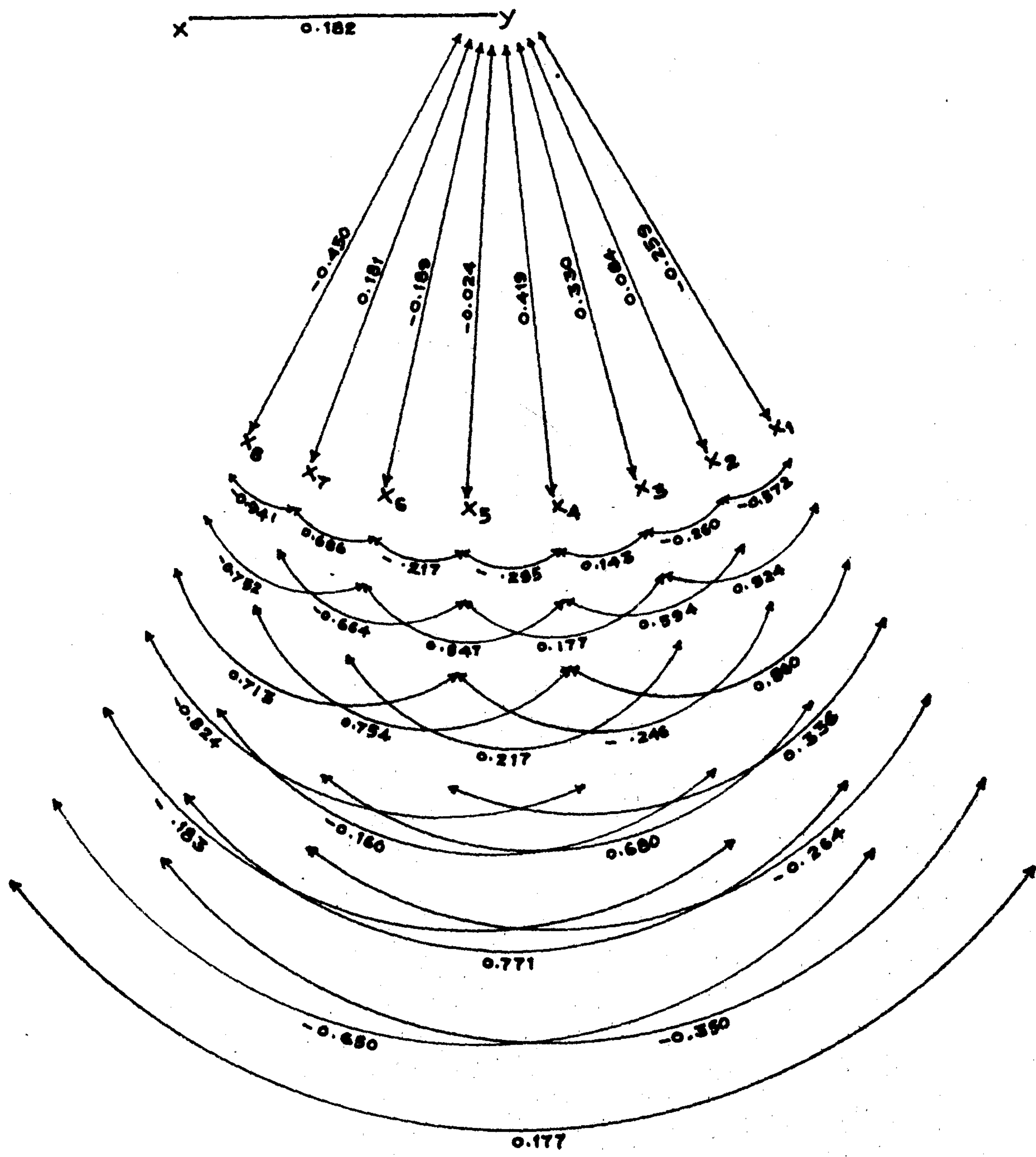
→ Direct effects.	X_3 Total soluble carbohydrates.
↔ Path coefficients.	X_4 Time factor.
x Residual effects.	X_5 Temperature.
y Flower bud differentiation.	X_6 Humidity.
X_1 C/N ratio.	X_7 Rain fall.
X_2 Nitrogen.	X_8 Sunshine hours.

Table 4.- Path coefficients of various factors contributing to flower bud differentiation in pepper (*Piper nigrum* L.) (Laterals that did not bear the crop during the past season)

Factors	Effect through								
	Total soluble carbo-hydrates	Nitrogen	C/N ratio	Time factor	Tempe-rature	Humi-dity	Rainfall	Sun-shine hours	Correla-tion with flower bud differen-tiation
Total soluble carbohydrates	<u>0.33</u>	-0.02	-0.24	0.06	-0.00004	0.004	-0.03	0.01	-0.13
Nitrogen	-0.09	<u>0.08</u>	0.15	0.25	0.01	-0.13	0.14	0.30	0.76
C/N ratio	0.30	-0.05	<u>-0.26</u>	-0.04	-0.0008	0.05	-0.06	-0.08	-0.13
Time factor	0.05	0.04	0.22	<u>0.42</u>	0.01	-0.16	0.14	0.37	0.89
Temperature	0.0005	-0.02	-0.01	-0.12	<u>-0.02</u>	0.04	-0.12	-0.32	-0.57
Humidity	-0.01	0.06	0.07	0.35	0.01	<u>-0.19</u>	0.12	0.34	0.75
Rain fall	0.05	0.06	0.09	0.32	0.02	- 0.13	<u>0.18</u>	0.42	0.91
Sunshine hours	-0.01	-0.05	-0.05	-0.34	-0.01	0.14	-0.17	<u>-0.44</u>	-0.95

Underlined figures denote direct effects
Residual effects = 0.182

Fig. 2 - PATH DIAGRAM (LATERALS THAT DID NOT BEAR THE CROP DURING THE PAST SEASON)



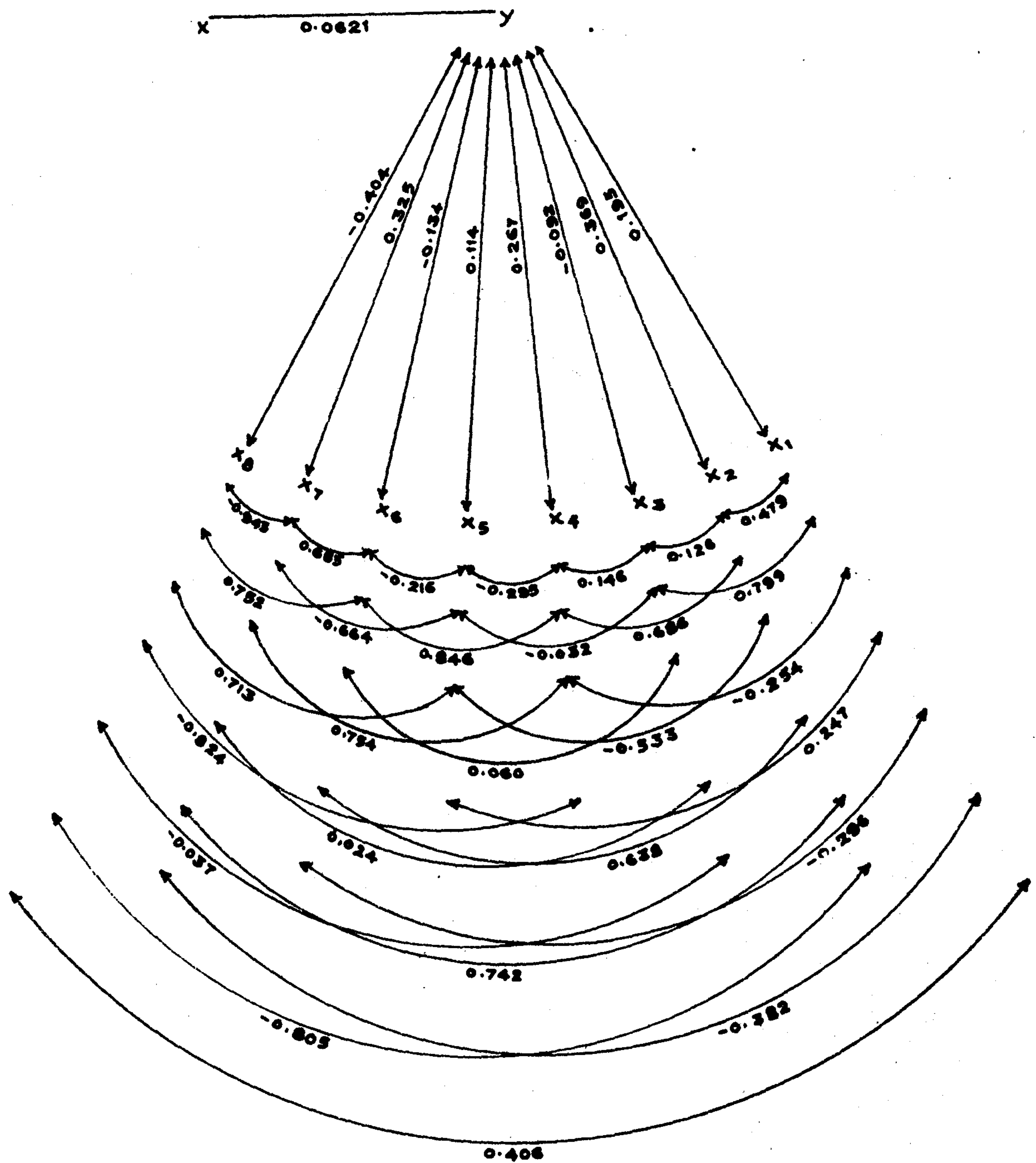
→ Direct effects.	X_3 Total soluble carbohydrates.
↷ Path coefficients.	X_4 Time factor.
X Residual effects.	X_5 Temperature.
Y Flower bud differentiation.	X_6 Humidity.
X_1 C/N ratio.	X_7 Rain fall.
X_2 Nitrogen.	X_8 Sunshine hours.

Table 5.- Path coefficients of various factors contributing to flower bud differentiation in pepper (*Piper nigrum* L.) (new shoots)

Factors	Effect through								
	Total soluble carbohydrates	Nitrogen	C/N ratio	Time factor	Temperature	Humidity	Rainfall	Sunshine hours	Correlation with flower bud differentiation
Total soluble carbohydrates	-0.09	0.05	0.16	0.04	-0.003	-0.01	0.01	0.02	0.16
Nitrogen	-0.01	0.37	-0.09	0.18	-0.06	-0.09	0.24	0.31	0.87
C/N ratio	-0.01	-0.18	0.20	-0.07	0.03	0.04	-0.12	-0.16	-0.34
Time factor	-0.01	0.25	-0.05	0.27	-0.04	-0.11	0.24	0.33	0.89
Temperature	0.003	0.20	0.05	-0.08	0.11	0.03	-0.22	-0.29	-0.58
Humidity	-0.01	0.24	-0.06	0.23	-0.02	-0.13	0.22	0.30	0.76
Rain fall	-0.002	0.27	-0.07	0.20	-0.08	-0.09	0.32	0.38	0.94
Sunshine hours	0.003	-0.30	0.08	-0.22	0.08	0.10	-0.31	-0.40	-0.96

Underlined figures denote direct effects
Residual effects = 0.062

Fig. 3 - PATH DIAGRAM (NEW SHOOTS)



→ Direct effects.	X_3 Total soluble carbohydrates.
↔ Path coefficients.	X_4 Time factor.
X Residual effects.	X_5 Temperature.
Y Flower bud differentiation.	X_6 Humidity.
X_1 C/N ratio.	X_7 Rainfall.
X_2 Nitrogen.	X_8 Sunshine hours.

rainfall (0.32) (Table 5, Fig.3). Total soluble carbohydrates had the minimum direct effect (-0.09). The indirect effects of nitrogen, time factor, temperature, humidity and rainfall through sunshine hours were high and it was more than its direct effect except for nitrogen and C/N ratio. Sunshine hours had the maximum correlation (r= -0.96) with flower bud differentiation followed by rainfall (r=0.94) and time factor (r=0.89).

4.2. HISTOLOGICAL STUDIES

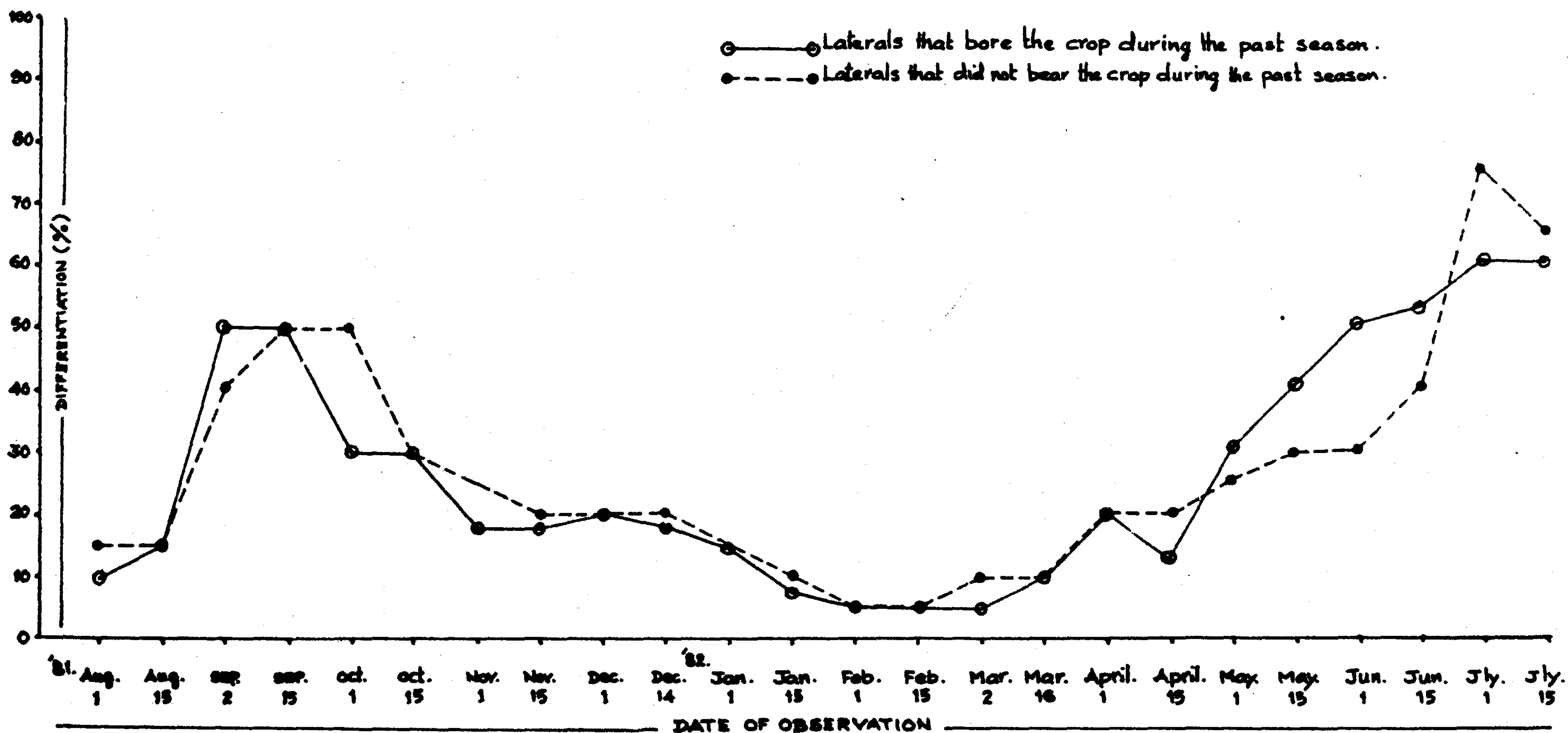
Studies were carried out in the two types of laterals (those that bore the crop during the past season and those that did not) and in the new shoots. During the 12-month period of observation, flower bud differentiation could not be observed in the two types of laterals. Initiation of vegetative buds was observed in the laterals.

4.2.1. Differentiation of vegetative buds

The data on initiation of vegetative buds in the two types of laterals are presented in Table 6 and in Fig.4.

Initiation of vegetative buds was found throughout the period of study. Maximum initiation of vegetative buds was found during twentyfirst to twentyfourth fortnight in both the types of laterals (50.0 to 60.0 per cent in case of the laterals that bore the crop during the past season and

Fig. 4 - DIFFERENTIATION OF VEGETATIVE BUDS IN THE TWO TYPES OF LATERALS



30.0 to 75.0 per cent in case of the laterals that did not bear the crop during the past season). This was followed by third to sixth fortnight (30.0 to 50.0 per cent in both types of laterals). Minimum initiation of vegetative buds (5.0 to 7.5 per cent) was recorded during the period between eleventh and fifteenth fortnight. In the laterals that bore the crop during the past season and between twelfth and sixteenth fortnight (5.0 to 10.0 per cent) in the laterals that did not bear the crop during the past season,

4.2.2. Stages of differentiation of vegetative bud

Vegetative buds were found to be axillary in position. The branching was apparently dichotomous. Shoot primordia were seen to arise from the axil of the main stem just below the nodes as undifferentiated conical meristem surrounded by leaf sheaths. Leaf sheaths were found to be elongated, conical structures (Plate 1).

The young shoot primordium was comprised of an outer tunica (one layer) and inner corpus. Spiral xylem vessels were present in abundance below the vegetative shoot primordia.

During stage II, the undifferentiated meristem and leaf sheaths were elongated (Plate 2).

Soon after this stage, the apical meristem started differentiation (Plate 3). An undifferentiated group of

Plate 1.- L.S. of vegetative bud showing initiation of shoot primordium and leaf sheath primordium X 50

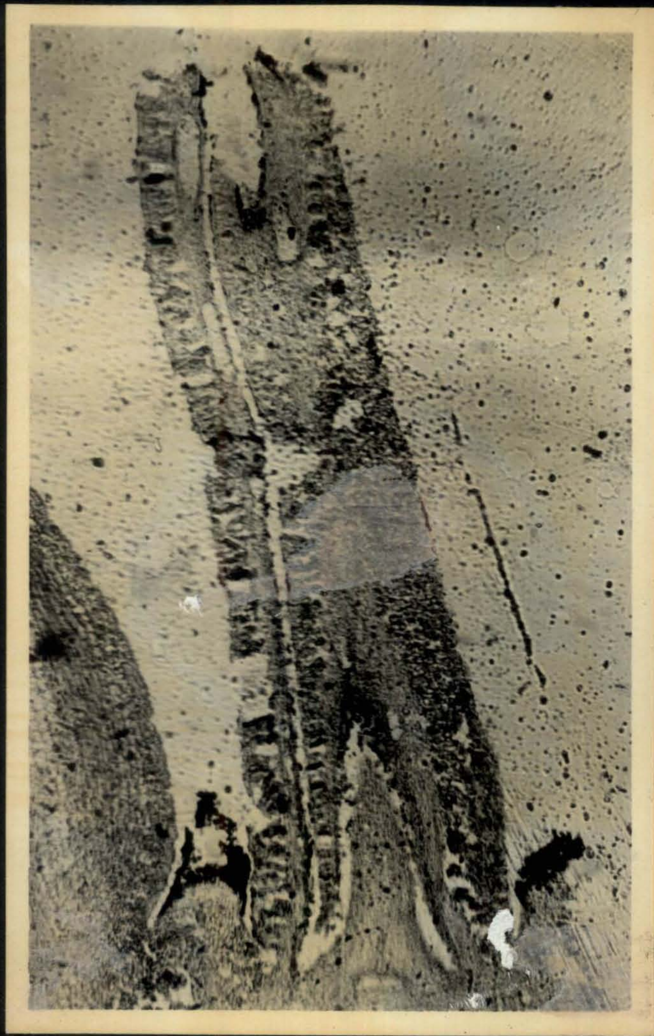


Plate 2.- L.S. of vegetative bud showing elongation of shoot primordium X 50

Plate 3.- L.S. of vegetative bud showing differentiation of shoot primordium X 50

initials was found at the terminal portion of the apical meristem. Below the undifferentiated group of initials, the following three different zones could be recognised:

i) Outer dermatogen like zone

ii) Inner periblem like zone

iii) Plerome like zone in the centre

Spiral xylem vessels were present below the apical meristem.

4.2.3. Differentiation of flower buds

Flower bud differentiation could not be observed in the two types of laterals (laterals that bore the crop during the past season and laterals that did not). However as presented in Table 7, flower bud differentiation was observed in the new shoots arising from the two types of laterals.

First evidence of flower bud differentiation was observed during the seventh fortnight. During the months of January, February and March, the percentage of buds differentiating into flower buds was comparatively low (5.0 to 12.5%). The percentage rose to about 40.0 by the beginning of June. All the buds examined from the laterals that bore the crop during the past season were seen to have differentiated into flower buds during the month of July. In the case of laterals that did not bore the crop during the past season, more

than 80.0% of the buds examined showed differentiation into flower buds.

4.2.4. Stages of differentiation of flower buds

The different stages of flower bud development identified are given below.

Appearance of two undifferentiated conical primordia surrounded by leaf sheath was the first sign of flower bud initiation. During this stage, these primordia could not be distinguished from the vegetative primordia (Plate 4).

During the next stage, one of the primordia was seen slightly broadened and elongated. Procambial strands were found in this primordium. The two primordia were continued to be enclosed by the leaf sheath (Plate 5).

At the apex of the broadened primordium a dome-shaped structure with two protuberances on either side developed during the third stage. The conical primordium was also present at the side of the broadened primordium. The two structures were continued to be enclosed by the leaf sheath (Plate 6).

During the stage IV, the dome-shaped structure slightly elongated and emerged out laterally from the main axis (Plate 7).

The slightly elongated dome-shaped structure enlarged

Plate 4.- L.S. of flower bud showing initiation of spike primordium x 50

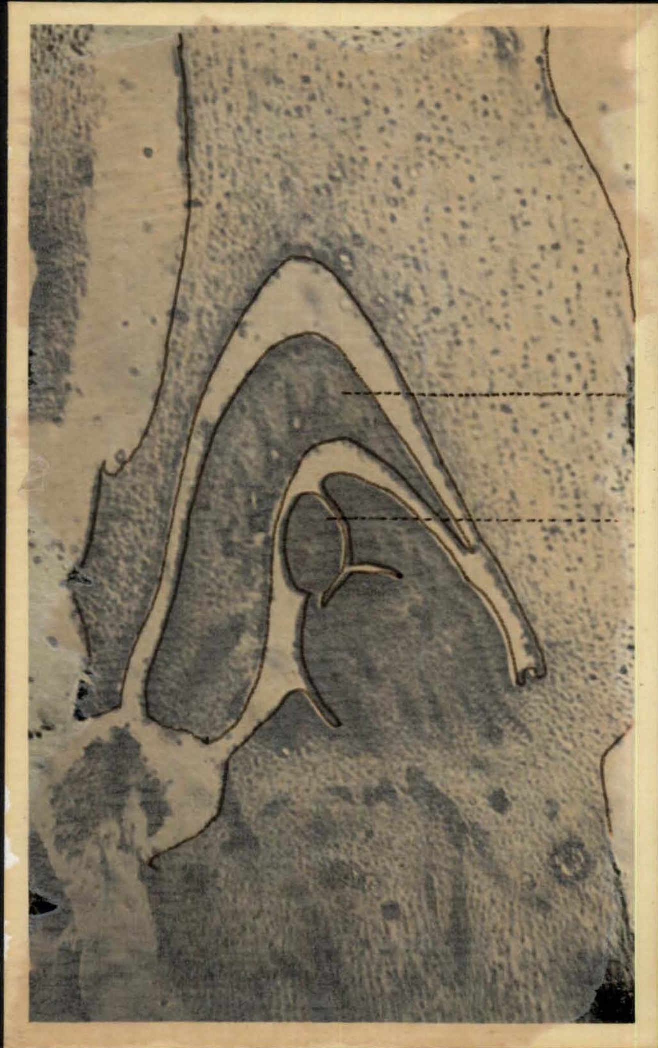


Plate 7.- L.S. of flower bud showing elongation of spike primordium X 50

into an elongated structure with lobbed margins during the fifth stage. This structure was covered by elongated leaf sheaths (Plate 8).

The structure enlarged and elongated further and a shape resembling the spike could be observed during the sixth stage. The lobbed nature of the margins was clear (Plate 9).

Flower primordia were seen to commence differentiation during this stage (Plate 10). Primordial bracts were found to be prominent. In the axil of each primordial bract, a small dome-shaped structure was observed.

During the stage VIII, the dome-shaped structures in the axils of the bracts enlarged in size (Plate 11). On either side of the dome shaped structures, protuberances developed. The bracts were seen elongated and enlarged and completely encircled the dome-shaped structure and the protuberances.

The stage IX revealed complete development of the pistils (Plate 12). The apical surface of the pistil showed a depression in the centre. Bracts were in the advanced stage of development.

Stamens and ovary could be identified at this stage. There were two stamens, one on either side of the ovary. The anther lobes and the filaments could be clearly identified (Plate 13).

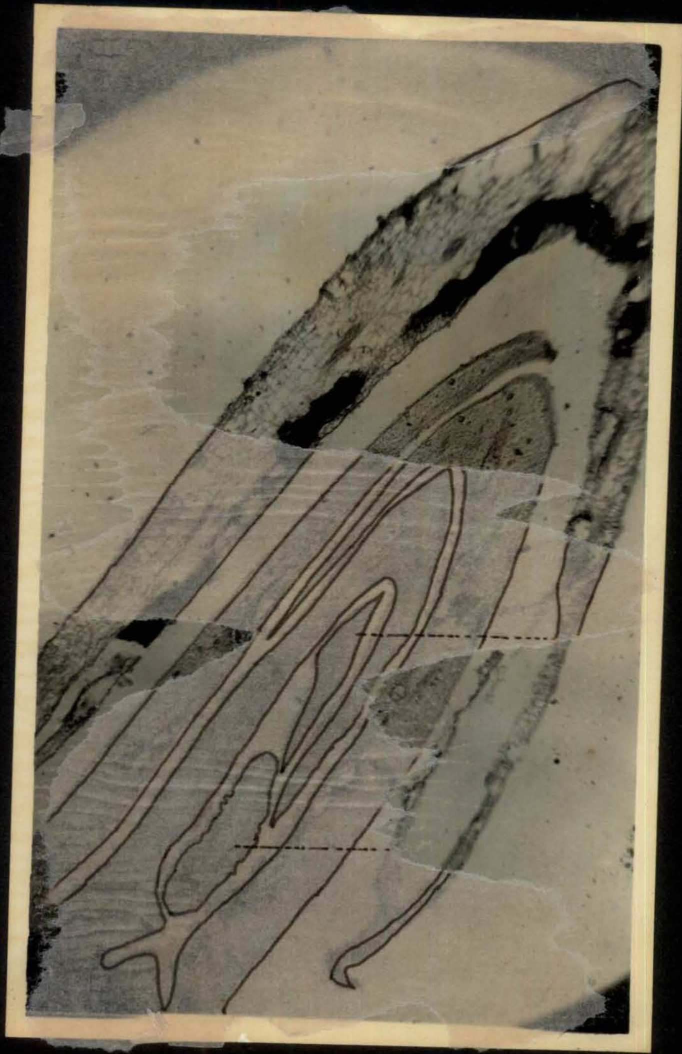


Plate 8.- L.S. of flower bud showing elongation of spike primordium X 50

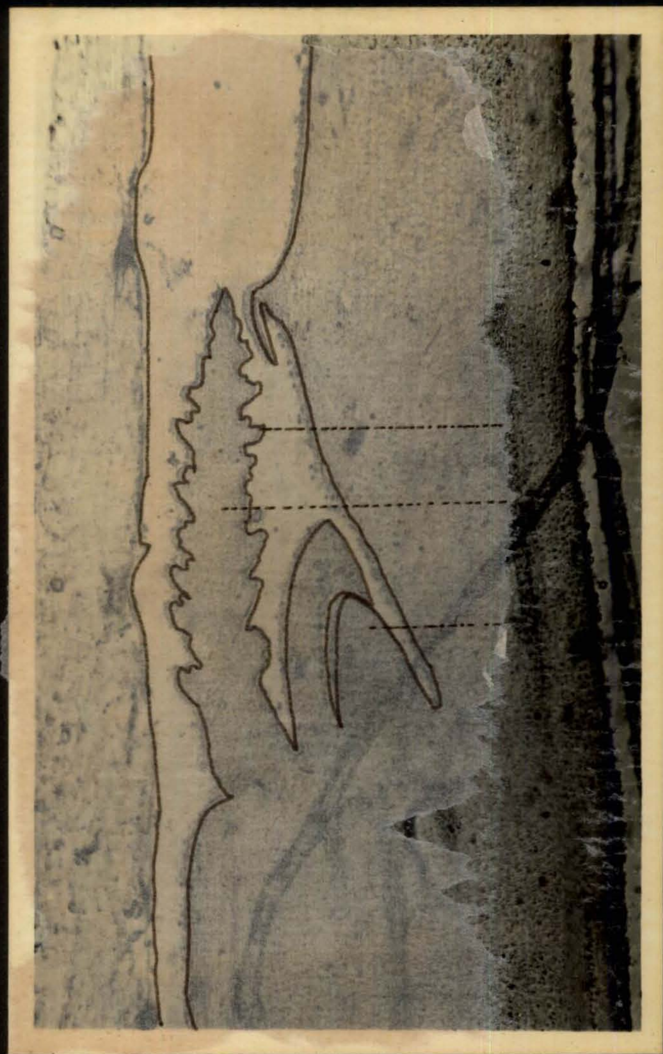


Plate 9.- L.S. of flower bud showing initiation of flower primordia in spike primordium X 50

Plate 10.- L.S. of flower bud showing bract primordia and pistil primordia X 50

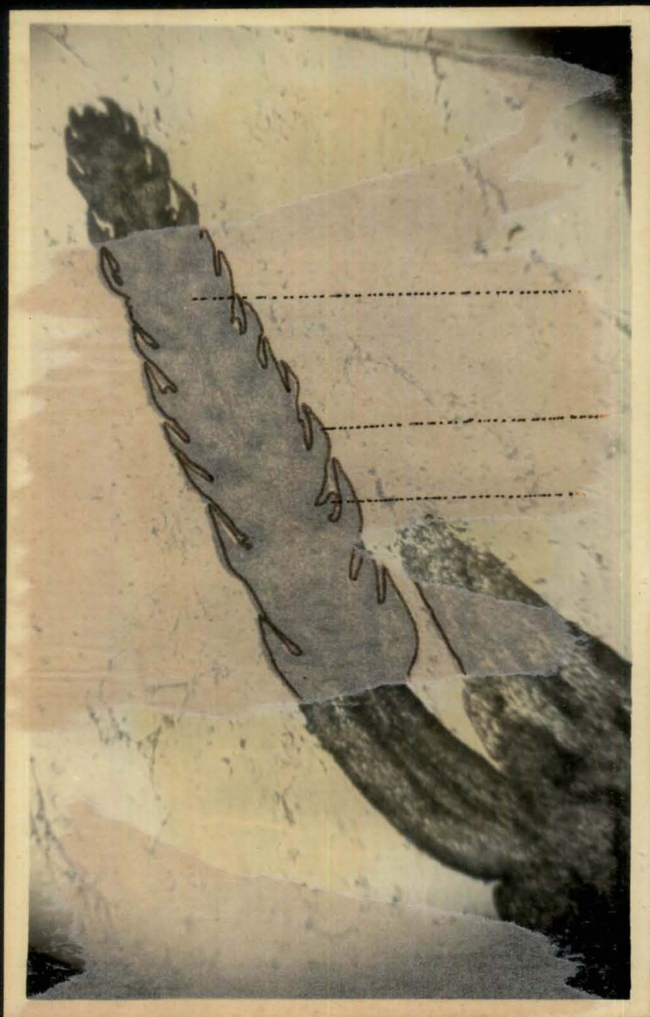


Plate 11.- L.S. of flower bud showing enlargement of bract primordia and pistil primordia X 10

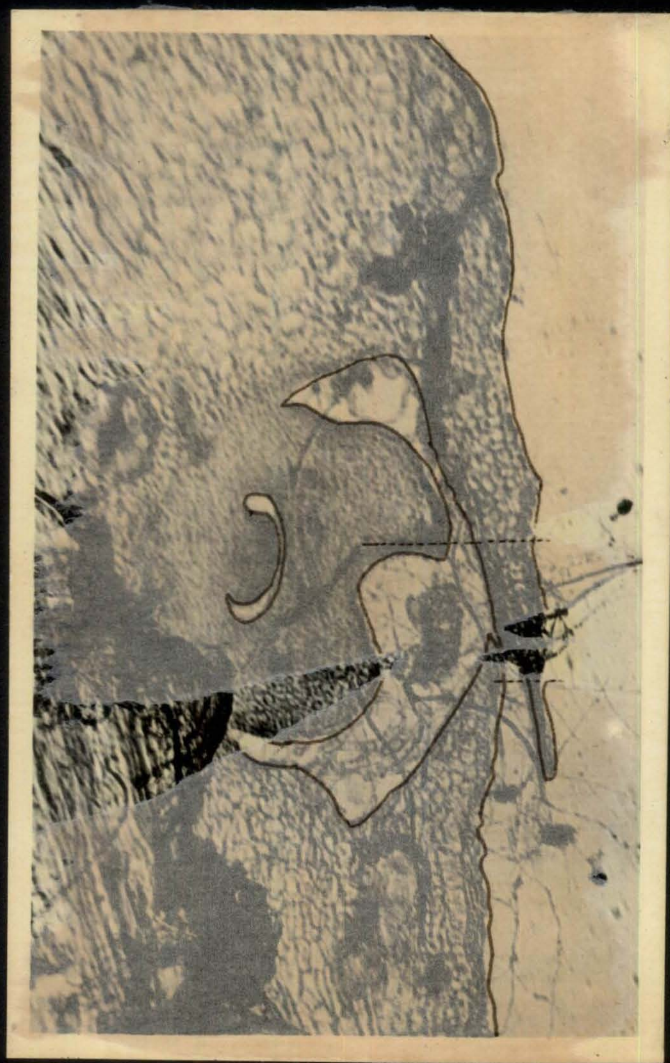


Plate 12.- L.S. of flower bud showing pistil X 100

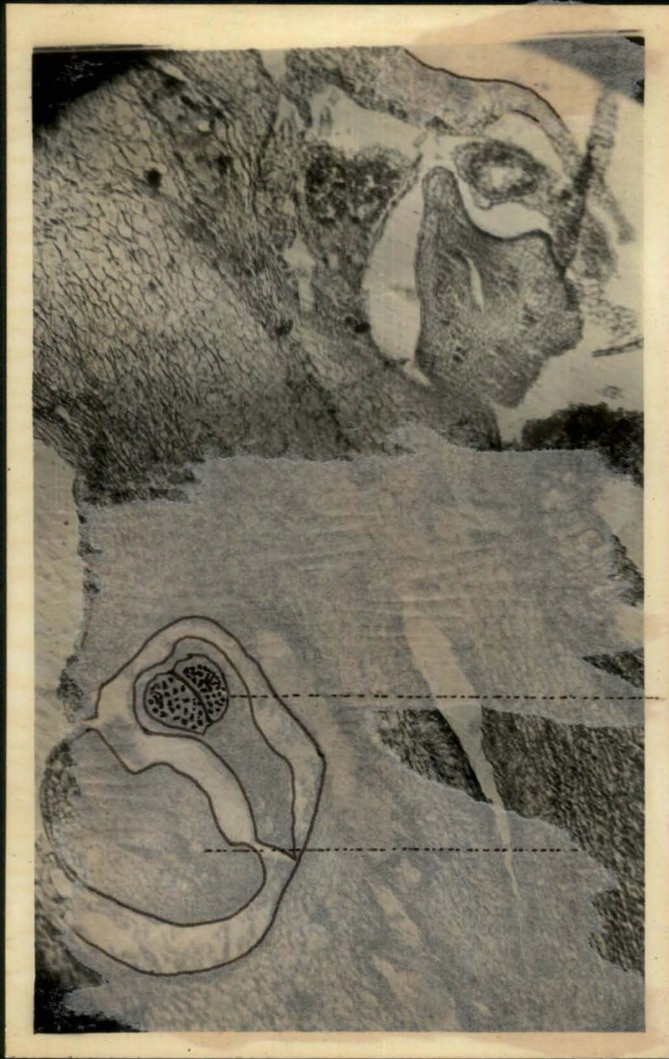


Plate 13.- L.S. of flower bud showing stamens and ovary X 100

4.2.5. Time taken for flower bud differentiation

Starting from 25.5.1982, ten buds from the laterals were extracted daily for examination so as to obtain information on the number of days taken for the different stages (from the initiation to completeness of flower bud differentiation).

The data presented in Table 8 seemed to indicate that the whole process of flower bud differentiation was completed within about 20 days of initiation. The initial stages (from stage 1 to stage 8) were completed within the buds and the later stages (from stage 8 to stage 10) after the bud break.

Table 8.- Number of days taken for the different stages* (Initiation to completeness of flower bud differentiation)

Internal developmental stages				Stages after bud break
Stage 1	Stage 3	Stage 6	Stage 8	Stage 10
D_2 to D_4**	D_5 to D_7	D_8 to D_{10}	D_{10} to D_{14}	D_{16} to D_{20}

* Based on ten shoot samples examined each day starting from 25.5.1982

** Stages observed during the days indicated

Discussion

5. DISCUSSION

Information on aspects of flower bud differentiation is the *sine qua non* for standardising and timing the various cultural and manurial operations of any perennial crop. Such information is practically lacking in pepper. Pepper bears the crop in the leaf axils of the current season's growth on the lateral branches. Flowering in pepper has been reported to be influenced by climatic factors, the predominant being rainfall. Generally, it is believed that flowering in pepper takes place on the receipt of 75 to 100 mm rain, after April. An off-season crop, though of minor importance, is often produced from October-November to March, again depending upon the rainfall and other climatic factors. In perennial crops, it is known that flower bud differentiation may take place a few days to several months before the emergence of the flowers. No information on flower bud differentiation and the factors influencing the differentiation is available in the case of pepper. Hence, the present studies were taken up at the College of Horticulture on six-year old pepper vines, cv. Panniyur-1. The studies consisted of two parts, one on the factors influencing flower bud differentiation and the other on the histological aspects of flower bud differentiation.

5.1. Factors influencing flowering/flower bud differentiation in pepper

The data presented in Table 1 and Fig.5 indicate that growth was minimum during the period between 15th December, 1981 and 15th February, 1982. The laterals did not record any extension growth during the month of March, 1982. Extension growth resumed only during the first week of April and continued till the 15th of July. Maximum extension growth was recorded during the months of June and July, these two months contributing to 86.56 per cent of the total growth in the laterals which bore the crop during the previous season and 82.52 per cent in the laterals which did not bear the crop during the previous season. The slow growth during the period from December, 1981 to the middle of March, 1982, can be considered as mainly due to the influence of climatic factors, especially the absence of rainfall. Data presented in Appendix I indicate that after a spell of dry weather, the experimental plants received rains from April. This led to the resumption of growth from April, 1982 onwards.

Analysis of the data on total soluble carbohydrates, nitrogen and C/N ratio of the two types of laterals and the new shoot, presented in Table 2, indicate considerable fluctuation in the carbohydrate and nitrogen levels (Fig.6, 7 and 8). The C/N ratio, though showed fluctuation, exhibited

Fig. 5 - FLOWER BUD DIFFERENTIATION IN RELATION TO - MEAN SHOOT EXTENSION GROWTH.

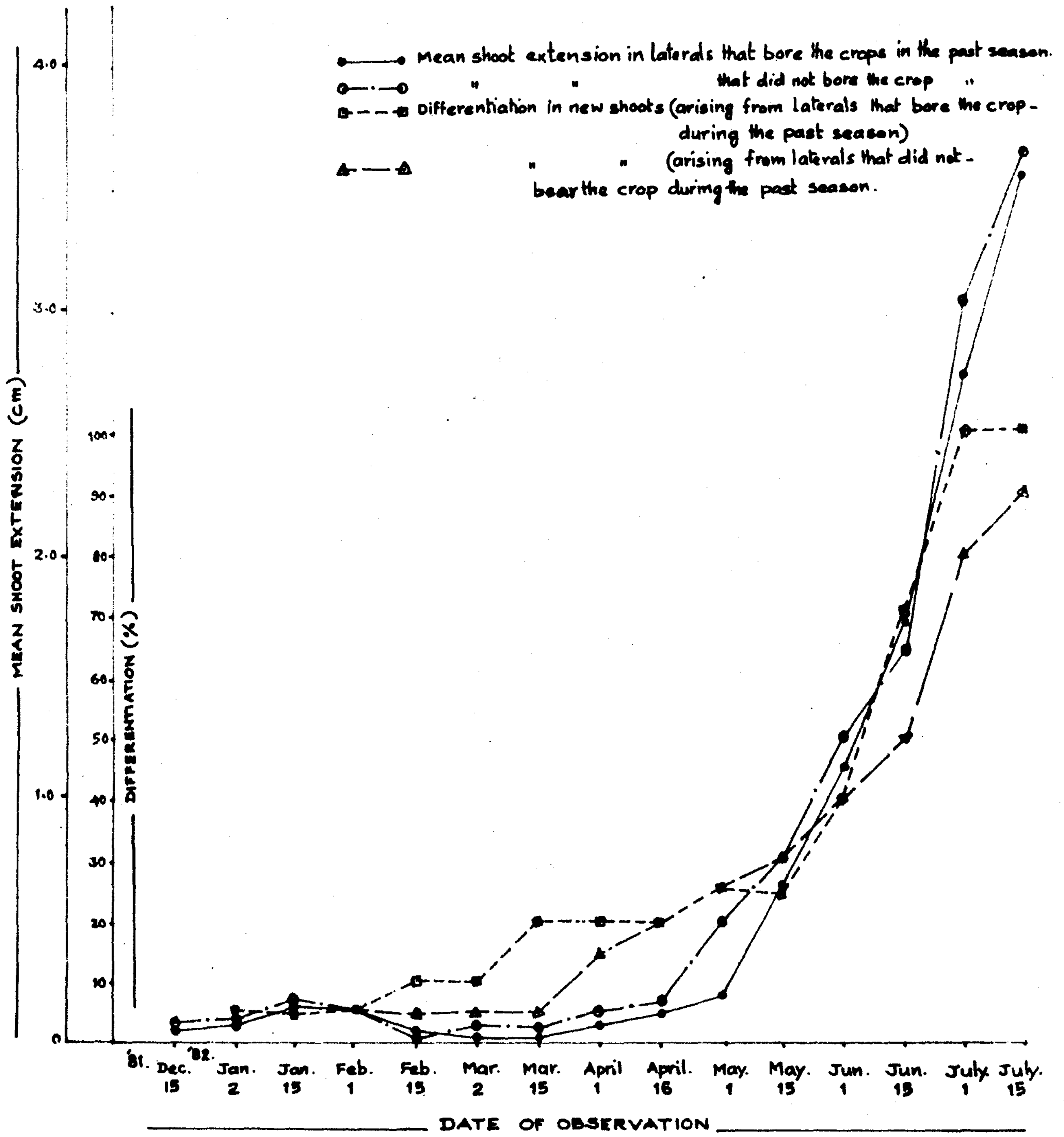
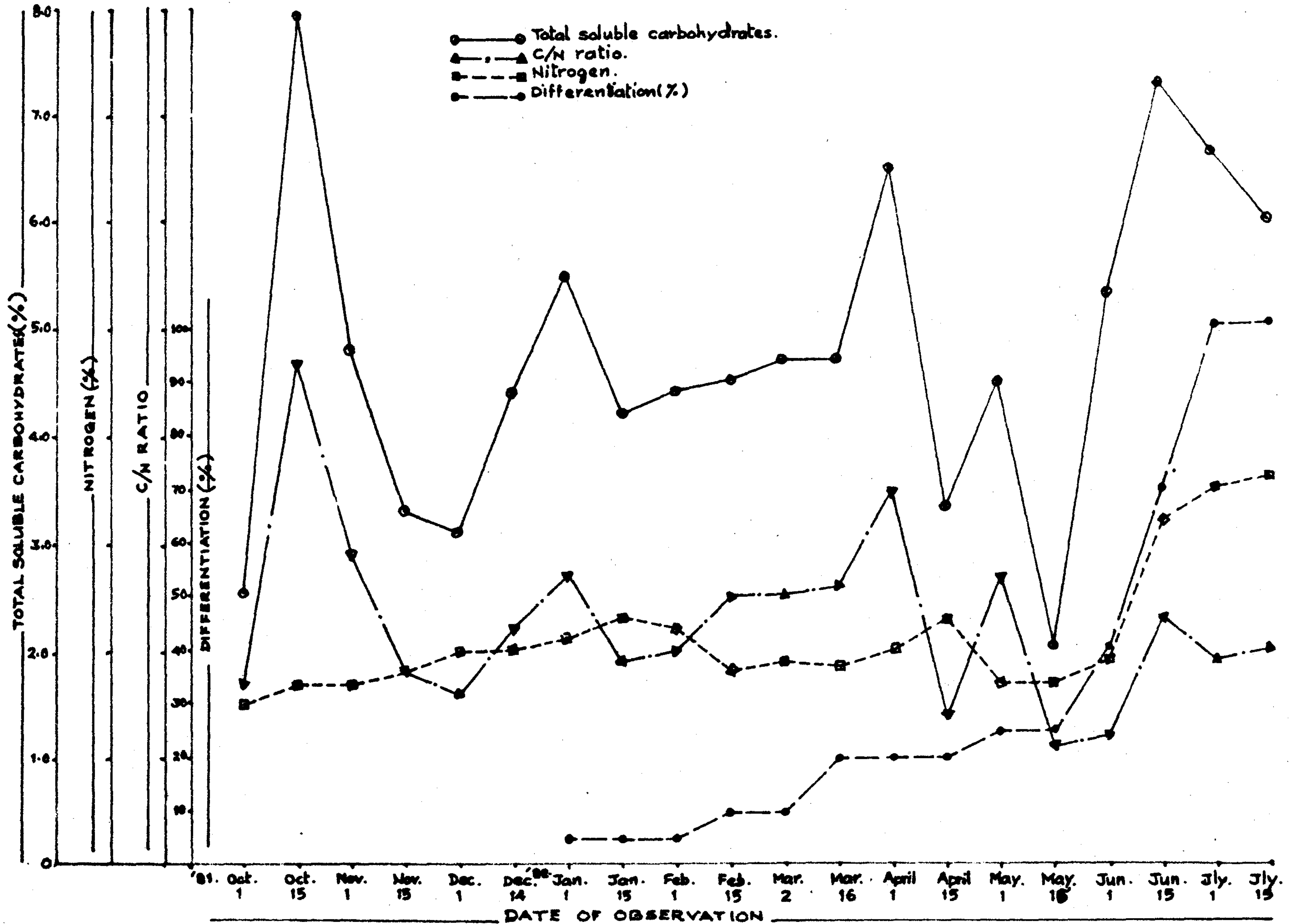


Fig. 6 - FLOWER BUD DIFFERENTIATION IN RELATION TO TOTAL SOLUBLE CARBOHYDRATES, NITROGEN AND C/N RATIO IN LATERALS THAT BORE THE CROP DURING THE PAST SEASON.



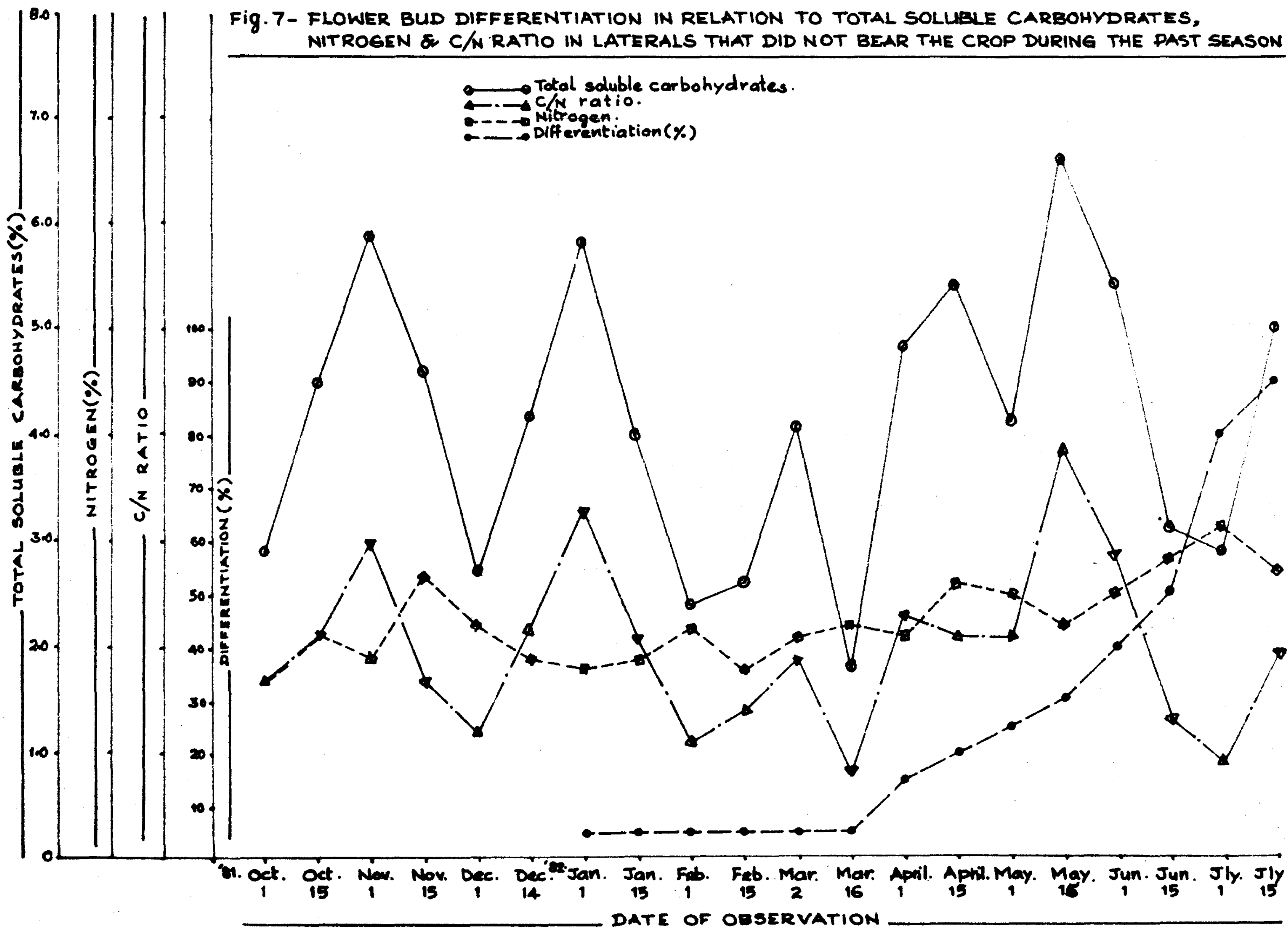
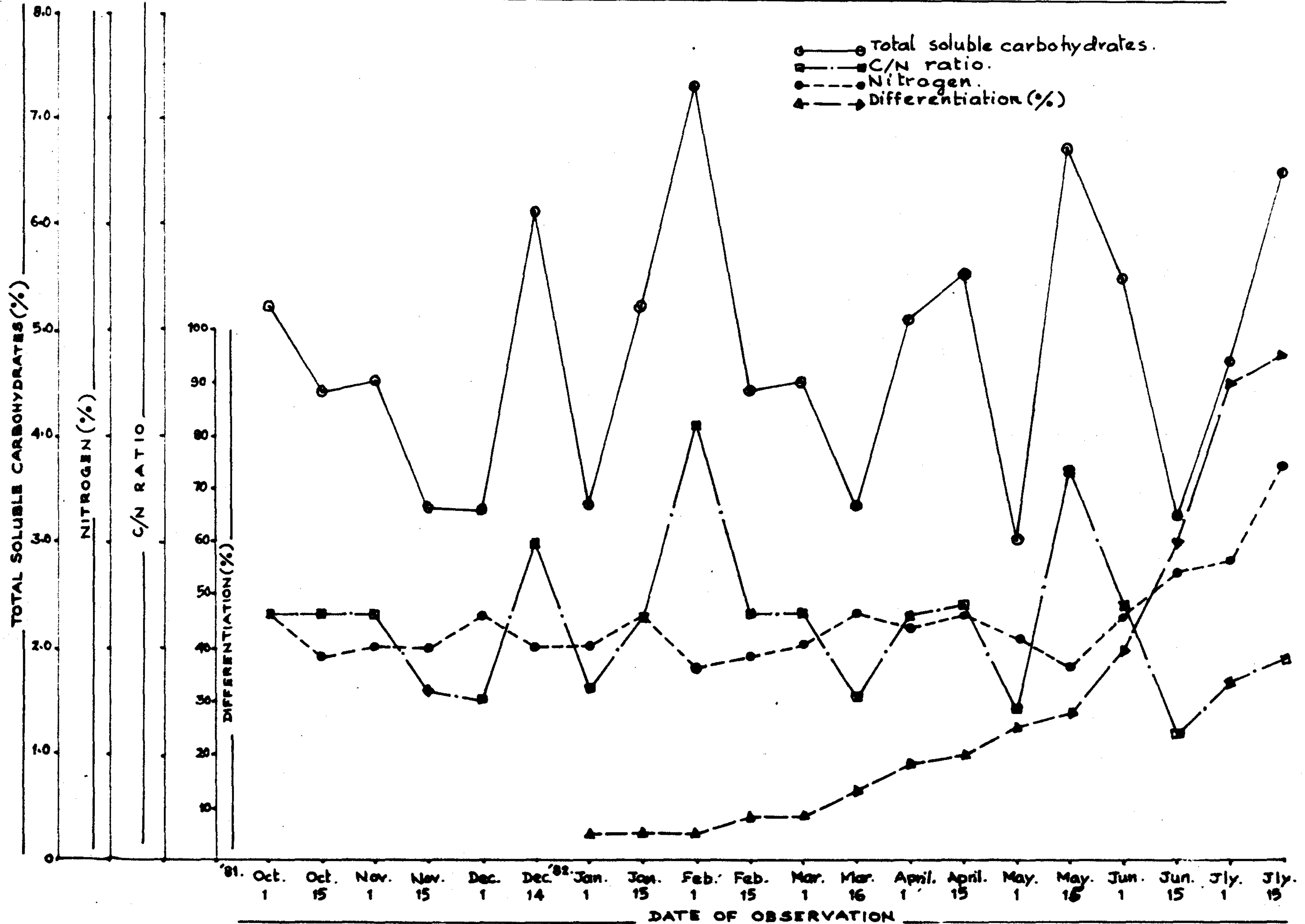


Fig. 7- FLOWER BUD DIFFERENTIATION IN RELATION TO TOTAL SOLUBLE CARBOHYDRATES, NITROGEN & C/N RATIO IN LATERALS THAT DID NOT BEAR THE CROP DURING THE PAST SEASON
Total soluble carbohydrates.
C/N ratio.
Nitrogen.
Differentiation (%)
TOTAL SOLUBLE CARBOHYDRATES (%)
NITROGEN (%)
C/N RATIO
DIFFERENTIATION (%)
8.0
7.0
6.0
5.0
4.0
3.0
2.0
1.0
0
100
90
80
70
60
50
40
30
20
10
'81. Oct. 1
Oct. 15
Nov. 1
Nov. 15
Dec. 1
Dec. 14
'82. Jan. 1
Jan. 15
Feb. 1
Feb. 15
Mar. 2
Mar. 16
April. 1
April. 15
May. 1
May. 16
Jun. 1
Jun. 15
Jly. 1
Jly. 15
DATE OF OBSERVATION

Fig. 8 - FLOWER BUD DIFFERENTIATION IN RELATION TO TOTAL SOLUBLE CARBOHYDRATES, NITROGEN AND C/N RATIO IN NEW SHOOTS.



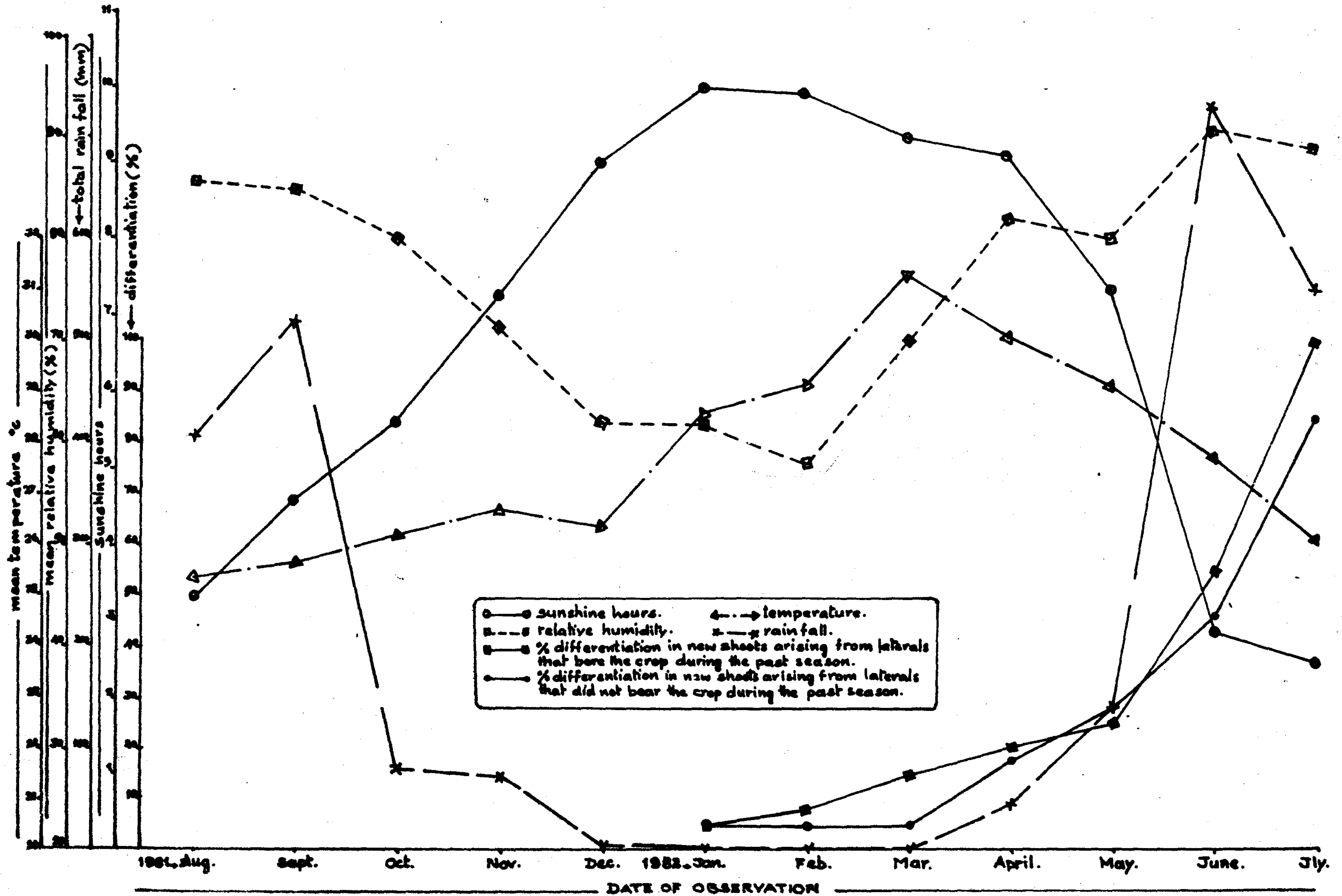
two peaks - October 15th and April 1st in the laterals which bore the crop during the previous season, January 1st and May 15th in the laterals which were unproductive during the previous season and February 1st and May 15th in the new shoots. The first peaks indicated the build up of carbohydrates and nitrogen which might have triggered the differentiation process, at least in the laterals that were unproductive during the past season. Appearance of the second peaks (April 15t , May 15th and May 15th) synchronised with the increase in the flower bud initiation activity of the plants. It was also observed that the C/N ratio reached the lowest levels by July 1st and June 15th in the laterals which were unproductive during the previous season and in the new shoots (Fig.7 and 8). In the laterals which were productive during the previous season, the lowest level was reached by May 15th (Fig.6). Though no significant correlation was obtained between C/N ratio and flower bud differentiation, the data seemed to indicate that it had a favourable influence on flower bud differentiation which is in tune with the existing knowledge on C/N ratio. Kraus and Kraybill established the effect of C/N ratio on flowering as early as in 1918. Since then, several workers studied the effect of C/N ratio on flower bud initiation/flowering. In grapes (Shantha, 1965; Chadha and Cheema, 1971; Rao and Sathyanarayana, 1978), mango (Naik and Shaw, 1937; Sen, 1946; Mallik, 1953;

Singh, 1960; Sen *et al.*, 1963) and jasmine (Subramanian and Shanmugavelu, 1981) similar observations have been made indicating the favourable role of C/N ratio on the flower initiation process.

A perusal of the data on weather parameters (Appendix I and Fig.9) will indicate that the temperature varied from 25.4°C to 31.3°C during the period of study. It can be observed that throughout the period of study, the temperature was above 25°C, which is higher than the minimum required for growth in pepper. The data also indicate that the months from December, 1981 to February, 1982 recorded relative humidities less than 62 per cent whereas the months of April, May, June and July, 1982 recorded relative humidities above 80 per cent. The rainfall figures indicate that during the months of May, June and July, 1982, the experimental plants received heavy rains (a total of 1425.8 mm). From the foregoing, it may be postulated that the rains in May triggered the flower bud initiation process in the physiologically mature shoots in which C/N ratio was built up to the required level.

Path coefficient analysis was done to assess the direct and indirect effects of total soluble carbohydrates, nitrogen, C/N ratio, time factor and the weather parameters - temperature, humidity, rainfall and sunshine hours on flower bud

Fig. 9- FLOWER BUD DIFFERENTIATION IN RELATION TO TEMPERATURE, HUMIDITY, RAINFALL & SUNSHINE HOURS.



differentiation in pepper. Data presented in the Tables 3 to 5 and the Figures 1 to 3 indicate that the eight factors studied accounted for more than 95 per cent variation. The residual effects were practically negligible. Among the eight factors studied, the hours of sunshine had the maximum correlation (negative) with flower bud differentiation. Rainfall exhibited the next highest correlation (positive).

A careful study of the weather data presented in Appendix I and Fig.9 along with the results of the path coefficient analysis indicate that rainfall may be critical for flower bud differentiation in pepper. The substantial quantity of rain received upto September, 1981 encouraged the vegetative growth and the build up of carbohydrate reserves which might have led to the first peak observed between October, 15th to February, 1st. This was followed by the absence of rain during the period from December, 1981 to March, 1982, which might have brought about the physiological ripening of the shoots, which is a pre-requisite for initiation of flower buds. Immediately following the receipt of pre-monsoon showers in April, 1982, a spurt of flower bud differentiation activity was observed. Maximum flower bud differentiation occurred during June-July, 1982. The above facts indicate that rainfall could be a predominant factor in influencing flower bud differentiation in pepper.

The observations reinforced the belief that pepper vines will flush and produce a crop after the receipt of 75-100 mm rainfall following a period of low rainfall or drought.

The data on duration of sunshine hours indicate that during the months of June, July and August the sun shined only for a few hours each day (less than 3.5 hrs). The overcast and cloudy sky in these months might have been responsible for the low sunshine hour values obtained. The study, being the first of its kind, does not conclusively reveal any role of sunshine hours on flower bud differentiation in pepper.

5.2. Histological studies

The second part of the study aimed at gathering information on the morphogenetic changes associated with flower bud differentiation in pepper. Since no work of similar nature was reported in pepper, the microtechnique had to be standardised first. Based on indications from other works, three killing and fixing fluids, two dehydration series, two embedding processes and two staining schedules were compared. Based on the rapidity of killing, absence of distortion and structural disturbances, and ability to render the material firm enough to withstand further handling, FAA was selected as the most suitable killing and fixing fluid.

Further, the facts that the specimens in FAA did not need washing before dehydration, and that the specimens could be stored in FAA for considerable length of time weighed in its favour. FAA has been reported suitable for grapes (Bernard, 1932; Snyder, 1933), red raspberry (Haltwick and Struckmeyer, 1947), citrus (Randhawa and Dinsa, 1947), jaman (Mishra and Bajpai, 1973), mango (Gunjate et al., 1977), strawberry (Pathak and Singh, 1977) and jasmine (Subramanian and Shanmugavelu, 1981). With regard to dehydration of the specimens, TBA series (Johansen, 1935) gave the best results. The specimens dehydrated by TBA series showed very little shrinkage of protoplasm and distortion of cells. TBA method has been recommended for blueberry (Aalders and Hall, 1964), mango (Gunjate et al., 1977) and strawberry (Pathak and Singh, 1977; Sharma and Singh, 1980). Embedding the specimens in the mixture suggested by Hance (1933) was found to give ideal sections during microtoming. Between the two types of staining schedules followed, the Saffranin series gave satisfactory results. Double staining by Saffranin-Fast Green series did not give encouraging results. However, this combination gave best results in citrus (Randhawa and Dinsa, 1947), mango (Gunjate et al., 1977) and strawberry (Pathak and Singh, 1977; Sharma and Singh, 1980). It is to be admitted that further work on double staining/multiple staining of pepper specimens is required before rejecting the Saffranin-Fast Green schedule.

Histological studies were carried out in the two types of laterals (which bore the crop during the previous season and which did not) and in the new shoots. The studies did not indicate flower bud differentiation in the two types of laterals. Vegetative initiation was observed in the laterals throughout the period of study, though at varying degrees. Maximum differentiation of vegetative buds occurred during June-July (Table 6). This may be explained as due to the high rainfall (1286.6 mm) received during this period. The September-October period in which the plants obtained reasonably good rainfall (608.2 mm) also recorded appreciable vegetative bud differentiation. Poor differentiation of vegetative buds obtained during the months of January, February and March can be explained as due to the lack of rainfall.

Three stages were identified in the development of vegetative buds. At the beginning of initiation, the vegetative primordium was conical, undifferentiated and surrounded by leaf sheaths (Plate 1). During the next stage (Plate 2), elongation of the primordium could be observed. This was followed by the differentiation of tissues at stage 3 (Plate 3). The three zones observed in the primordium during this stage were the outer dermatogen like zone, the inner periblem like zone and the central plerome like zone. Detailed studies are warranted to elucidate further information on

these aspects. As early as in 1870, Hanstein had postulated that the apical meristem of angiosperms consisted of three parts, the outermost, the dermatogen (which would develop into the primordial epidermis), the periblem (which would give rise to the cortex) and the plerome (which would constitute the entire inner mass of the axis). Dermatogen and the periblem formed mantle like layers covering the plerome. Conical nature of the vegetative primordia was observed in several other crops such as grapes (Chadha and Cheema, 1977), mango (Singh, 1960), jamun (Mishra and Bajpai, 1973) and strawberry (Pathak and Singh, 1977). However, distinct stages were not observed in the differentiation and development of vegetative buds in mango (Singh, 1960).

Flower bud differentiation was observed only in the new shoots arising from the two types of laterals. The laterals themselves did not show flower bud differentiation. This indicates that flower bud differentiation occurred along with or immediately after the vegetative growth in the season. In citrus, flower bud initiation was observed to synchronise with the initiation of growth in the spring (Abbot, 1935; Ahamad and Khan, 1951). In mango, flower bud differentiation was observed to be during October-November and in the mature current season's growth (Sen and Mallik, 1941). However, flower bud differentiation in grapes was observed to be during

the season preceding the fruiting season (Bernard, 1932; Rajaram et al., 1964; Chadha and Cheema, 1971).

Data on flower bud differentiation have been presented in Table 7. During the months of January, February and March, the percentage of buds differentiating into flower buds was negligible (5.0 to 7.5 per cent). Flower bud differentiation during this period can be explained as due to the favourable build up of C/N ratio. This would have resulted only in a minor off-season crop. Immediately following the receipt of pre-monsoon showers, a spurt in the flower bud differentiation activity was observed. Maximum (40.0 to 95.0 per cent) flower bud differentiation was observed during June-July. The fact that the two types of laterals (which bore the crop during the previous season and which did not) examined did not exhibit significant flower bud differentiation indicates that under normal cultural and manurial practices, the crop load of previous season had probably no influence on flower bud differentiation during the succeeding season. It is pointed out that the vines used in the experiment were only six years old and had not attained the peak bearing age. As such, the depletion effects due to a heavy crop could not have played a role. More detailed studies are required to confirm whether or not crop load in a season has any influence on the flower bud differentiation during the ensuing season. In other crops,

the review has shown evidences in both directions.

The histological examination revealed the details of initiation and development of flower buds. The ten stages observed could be recognised into five developmental stages. During the first developmental stage, appearance of two undifferentiated conical primordia surrounded by a leaf sheath was observed (Plate 4). Initially, the two primordia were similar in shape and as such the vegetative and the floral primordia could not be distinguished. Towards the latter half of the first stage, one of the primordia broadened and elongated (Plate 5). Procambial strands were formed in this primordium which could be recognised as the floral primordium. This developmental stage marked the commencement of the flower bud differentiation process. Broadening and flattening of the apical meristem just before flower initiation has been observed in citrus (Abbot, 1935; Randhawa and Dinsa, 1947; Mishra and Yamdagni, 1968; Babu and Kaul, 1972), litchi (Shukla and Bajpai, 1974) and strawberry (Pathak and Singh, 1977). In grapes, Chadha and Cheema (1971) observed that the leaf primordium was pointed whereas the cluster primordium was blunt and broad. Esau (1962) has stated that the small depth and comparatively broad expanse of the meristematic tissue are the common histologic features of the floral meristem. According to her, the broad apex would be occupied by a mantle of meristematic cells and beneath the mantle,

there would be a vacuolated core of ground tissue no longer connected with growth.

In the next stage, the broadened primordium developed a dome-shaped structure at its apex with two protuberances on either side (Plate 6). Towards the latter half of the second stage, the dome-shaped structure elongated and emerged out laterally from the main axis (Plate 7). The dome-shaped structure would later develop into the spike primordium and the two protuberances on either side into the bract primordia. This developmental stage denoted the spike initiation.

The dome-shaped structure further enlarged, elongated and formed lobbed margins during the third stage. A shape resembling the pepper spike could be observed (Plate 8). The lobbed nature of the structure was due to the presence of the flower primordia. The elongation of the spike primordium continued and the lobbed nature of the margins became intense during the mid-stage III (Plate 9). The third stage thus indicated floral initiation.

During the fourth stage, the bract primordia were prominent. In the axil of each bract primordium, a small dome-shaped structure could be recognised which indicated the flower primordia (Plate 10). Later in the fourth stage, the bract and the flower primordia enlarged and two protuberances developed on either side of the dome-shaped structure

(Plate 11). In pepper, the flowers are reported to be bracteate without perianth (Benson, 1970; Rendle, 1971; Purseglove *et al*., 1981). The dome shaped structure may therefore be regarded as the pistil primordia. The two protuberances which developed on either side of the dome shaped structure were recognised as the stamen primordia. Pistil primordium was observed towards the end of the fourth stage (Plate 12). The apical surface of the pistil primordium showed a depression in the centre. This may be the stigmatic portion. The fourth stage showed the differentiation of the floral parts.

The stamens and the ovary could be clearly identified during the fifth stage (Plate 13). On either side of the ovary, one stamen each with two anther lobes could be observed. According to Rendle (1971), *Piper nigrum* has only two stamens. Cobley and Steele (1976) and Purseglove *et al*. (1981) have reported that two to four stamens occur on either side of the ovary in the hermaphrodite flowers. The ovary has been described as ovate, unilocular and superior (Cobley and Steele, 1976; Shukla and Mishra, 1979; Purseglove *et al*., 1981). The fifth developmental stage marked the completion of the flower bud differentiation activity.

In mango (Sen, 1943; Mustard and Lynch, 1946; Khan, 1960; Gunjate *et al*., 1977; Ravishankar *et al*., 1979) and strawberry

(Sharma and Singh, 1980), four stages have been recognised in the development of the fruit buds. In fig, Rane and Singh (1965) identified five stages in the differentiation of flower buds.

The floral parts developed in the order of bracts, pistil and stamen. It is not very clear from the studies whether the development of floral parts is in acropetal or basipetal succession. Further studies are required to clarify this point. Development of floral parts in acropetal succession in the sequence of sepals, petals, stamens and ovary has been observed in several crops such as grapes (Rajaram,1964), mango (Mustard and Lynch, 1946; Musahib-ud-din, 1946; Singh, 1958; Karandhikar, 1960; Sawant, 1969), Litchi (Shukla and Bajpai, 1974), strawberry (Pathak and Singh, 1977) and jasmine (Subramanian and Shanmugavelu, 1981).

The data presented in Table 8 seemed to indicate that the whole process of flower bud differentiation in pepper was completed within about 20 days. The first three stages were completed within the buds and the later two stages, after the bud break. Karandhikar (1960) and Gunjate et al. (1977) reported that the whole process of flower bud differentiation was completed in mango within two to two and half months. In citrus, the duration of flower bud differentiation was observed to be 15 days (Ahamad and Khan, 1951; Mishra and

Yamdagni, 1968). In apple, about four to five months (Gyuro, 1959; Marrow, 1962; Neumann, 1962; Feucht and Arancibia, 1970) and in strawberry 25 to 30 days (Pathak and Singh, 1977) were required for completion of flower bud differentiation.

Summing up, the studies revealed that C/N ratio had a favourable influence on the differentiation of flower buds in pepper. Results of the path coefficient analysis and the data on the weather parameters considered together indicated rainfall as the critical factor influencing flower bud differentiation in pepper. Receipt of the pre-monsoon showers after a long spell of dry weather seemed to trigger the flower bud differentiation activity. The histological examination revealed three stages in the differentiation of vegetative buds and five in the differentiation of flower buds.

Summary

6. SUMMARY

6.1. Studies were undertaken at the College of Horticulture, Vellanikkara during 1981-82 to collect information on the factors influencing flowering/flower bud differentiation in pepper and on the chronological development of the vegetative and floral buds. The study being the first of its kind in pepper, there was need to standardise the microtechnique also.

6.2. Growth observations on the Panniyur-1 vines revealed that maximum extension growth (80 per cent) in the two types of laterals (which bore the crop during the previous season and which did not) occurred during the months of June and July while the growth was minimum (2 per cent) during the months of February and March.

6.3. Total soluble carbohydrates, nitrogen content and C/N ratio of the two types of laterals and the new shoots varied considerably during the growth cycle. Carbon-nitrogen ratio exhibited two peaks, the first synchronising with the commencement of the differentiation process and the second, with the step up of flower bud differentiation activity.

6.4. The data were further subjected to path coefficient analysis to assess the direct and indirect effects of

the nutrient status of the plants and the weather parameters on flower bud differentiation. The results showed that the eight factors studied accounted for more than 90 per cent of the variation. Among the variables, hours of sunshine was negatively correlated and the rainfall positively correlated with the flower bud differentiation. The results indicated that the rainfall was the most important factor influencing flower bud differentiation in pepper. It has been concluded that receipt of the pre-monsoon showers after the dry spell during December to April triggered the flower bud differentiation activity in pepper.

6.5. FAA has been found to be the most suitable killing and fixing fluid. With regard to dehydration of the specimens, TBA series gave the best results. Between the two types of staining schedules followed, the Saffranin series gave satisfactory results. Further work is, however, necessary for standardising double/multiple staining of pepper stem sections.

6.6. The histological studies carried out in the two types of laterals and in the new shoots, failed to show flower bud differentiation in the laterals. Differentiation of vegetative buds was observed in the laterals

throughout the period of study, though at varying degrees. Maximum differentiation of vegetative buds occurred during June-July (40.0 to 67.5 per cent) and minimum during January to March (5.0 to 15.0 per cent).

6.7. Three stages have been identified in the development of vegetative buds. Appearance of conical undifferentiated vegetative primordia surrounded by leaf sheaths marked the initiation. During the second stage, elongation of the primordia was observed. Differentiation of tissues into the outer dermatogen like zone, the inner periblem like zone and the central plerome like zone occurred at the third stage, indicating the completion of vegetative bud differentiation.

6.8. Flower bud differentiation was observed in the shoots arising from the two types of laterals. During the dry months of January, February and March, the percentage of buds differentiating into flower buds was found to be negligible (5.0 to 12.5). A spurt in the flower bud differentiation activity was observed immediately after the receipt of the pre-monsoon showers. Maximum flower bud differentiation occurred in June-July (40.0-95.0 per cent).

6.9. Five stages were identified in the development of flower buds. During the first stage, two undifferentiated conical primordia surrounded by a leaf sheath were observed indicating the commencement of flower bud differentiation process. Towards the latter half of the first stage, one of the primordia broadened and elongated. Appearance of a dome-shaped structure at the apex of the broadened primordium in the second stage denoted spike initiation. The third stage indicated floral initiation and a shape resembling the pepper spike could be clearly observed. During the fourth stage, differentiation of the floral parts was observed. Stamen and pistil primordia could be seen towards the end of the fourth stage. Completion of the differentiation process was indicated by the appearance of the stamens and the ovary during the fifth stage. It was not clear from the studies whether the development of floral parts was in acropetal or basipetal succession.

6.10. The studies seemed to indicate that the process of flower bud differentiation was completed within about 20 days of commencement.

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* Originals not seen

Appendix

APPENDIX -I

Weather data (monthly average) for the period from August, 1981 to July, 1982

Month	Temperature (°C)	Relative humidity (%)	Total rainfall (mm)	Sunshine hours
August, 1981	25.40	87.13	407.9	3.30
September	25.65	85.05	521.8	4.60
October	26.20	79.76	86.4	5.50
November	26.65	71.51	80.2	7.20
December	26.40	61.22	-	9.00
January, 1982	28.55	61.67	-	10.00
February	29.10	57.70	-	9.90
March	31.30	69.63	-	9.30
April	30.05	81.70	45.2	9.10
May	29.15	79.90	139.2	7.30
June	27.70	91.15	734.8	2.90
July	26.10	88.15	551.8	2.54

Source: 'B' Class Observatory, Vellanikkara

FLOWER BUD DIFFERENTIATION IN PEPPER (*Piper nigrum* L.)

By

P. V. NALINI

ABSTRACT OF THE THESIS

Submitted in partial fulfilment of the requirements for the degree of

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ABSTRACT

Studies were undertaken at the College of Horticulture, Vellanikkara during 1981-82 to collect information on the factors influencing flowering/flower bud differentiation in pepper and on the chronological development of the vegetative and floral buds.

Carbon-nitrogen ratio exhibited a favourable influence on the differentiation of flower buds in pepper. Results of the path coefficient analysis and the data on the weather parameters considered together indicated rainfall as the most important factor influencing flower bud differentiation. Receipt of the pre-monsoon showers after a long spell of dry weather seemed to trigger the flower bud differentiation activity in pepper.

Microtechniques for histological examination of pepper stem sections were standardised. Killing and fixing the specimens in FAA, dehydration in TBA series and staining with saffranin gave satisfactory results.

Differentiation of vegetative buds alone was observed in the two types of laterals (which bore the crop during the previous season and which did not). Three stages have been identified in the development of vegetative buds.

Flower bud differentiation was observed in the shoots arising from the two types of laterals. Maximum flower bud differentiation occurred during June-July. Five stages were identified in the development of flower buds. The process of flower bud differentiation was seen completed within about 20 days of commencement.