PHYSIOLOGICAL AND BIOCHEMICAL ASPECTS OF FLOWERING, BERRY SET AND DEVELOPMENT IN BLACK 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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**Department of Plantation Crops and Spices
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DECLARATION

I hereby declare that the thesis entitled "Physiological and biochemical aspects of flowering, berry set and development in black pepper (P*iper nigrum* L.)" is a bonafide record of research work done by me during the course of research and that the thesis has not previously formed the basis for the award to me of any degree, diploma, fellowship or other similar title, of any other University or Society.

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CERTIFICATE

Certified that the thesis entitled "Physiological and biochemical aspects of flowering, berry set and development in black pepper (*Piper nigrum* L.)" is a record of research work done independently by Mr. K.N. Satheeshan under my guidance and supervision and that it has not previously formed the basis for the award of any degree, diploma, fellowship or associateship to him.

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CERTIFICATE

We, the undersigned members of the Advisory Committee of Mr. K.N Satheeshan, a candidate for the degree of Doctor of Philosophy with major in Horticulture, agree that the thesis entitled "Physiological and biochemical aspects of flowering, berry set and development in black pepper (P*iper nigrum* L.)" may be submitted by Mr. K.N. Satheeshan, in partial fulfilment of the requirements for the degree.

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Introduction

INTRODUCTION

Improvement of black pepper has been slow over the years owing to high heterozygosity as well as long breeding cycle. Inspite of the strides in production technology, the gap between potential and realised yield is wide and the productivity of black pepper crop has consistently been low. The reasons attributed are the devastating disease and pest problems, the major being *Phytophthora* foot rot and slow wilt diseases, followed by fungal and insect pollu and physiological disorders. The crop is cultivated extensively in Kerala in an area of 2,38,320 ha (Madan, 2000) and is the mainstay of economy of the farmers of midlands and uplands. Out of the annual production of 65990 t (Madan, 2000), more than 60 per cent are exported, earning an exchequer of Rs.86498 lakh (Peter and Nybe, 2000) for the Country. The poor productivity in the order of 315 Kg ha^{-1} as against 4000 Kg ha^{-1} (Ghosh *et al.*, 1999) in Thailand warrants immediate interventions for improving productivity. The wide gap between the potential yield and realised yield gives sufficient proof that tremendous improvement in productivity is possible with the available technology. Understanding the basic mechanisms in productivity of this crop assume significance in this context.

Productivity of black pepper is highly dependent on the growth and flowering behaviour of the vine. Flowering and fruit set in black pepper presents a number of unique features, which is not seen in other tropical plantation and spice crops. The pattern is rhythmic, in which the growth during a season is initiated through flushing, resulting in extension growth and the rest period that follows. This is repeated in an annual cycle. Flowering occurs only in the current season growth of the lateral shoots known as plagiotropic branches. The main yield components in black pepper are determined during flushing and flowering. Hence to exploit the full production potential in black pepper, a detailed understanding of growth and flowering pattern is of great importance. For high productivity, various cultural practices will have to be timed in relation to their critical stages of growth, especially during flowering and fruit set. As such, an investigation on the role of various factors involved in flowering and fruit set will provide valuable information for crop production and scientific management in black pepper. This will enable us to reorient crop production technology through manipulation of the limiting factors, both external and internal, to bring forth the maximum flowering and fruit set.

Growth analysis has been proved to be highly effective in studying plant reaction to environmental condition and comparison between species (Poorter, 1991). Quantitative measurements of shoot growth and development such as morphological index (Hanson *et al.*, 1986) and plastochron index (Schultz, 1993 and Heuvelink, 1995) are more specific and reproducible. A similar study is required to identify the growth stages of the plant specific to black pepper. Adoption of systems for identifying phenological growth stages is also useful in developing crop growth models. Models predicting growth and development as a function of environmental factors can be used in production planning (Coombe, 1995 and Marcelis *et al.*, 1998).

Physical yield of a crop is determined by dry matter production and distribution by the leaves and the dry matter content of harvestable organs (Marcelis, 1996). In black pepper, berries form the economic part and the dry matter partitioned by them is important, as the produce is sold on dry weight basis rather than fresh weight. These factors also determine the product volume and product quality. The berries also play an important role in biomass accumulation, as they are the major sinks. An understanding on the regulation of carbon partitioning among sinks and its relation to plant growth and development is important for establishing strategies for increasing plant productivity.

Photosynthesis is the basic source of biomass accumulation. Moreover, a direct correlation exists between biomass and yield in many crops. The dry matter production also, is driven primarily by photosynthesis and the factors affecting the process. Therefore, it becomes essential to understand the regulatory process of photosynthesis. If some of the limiting factors could be identified, it would be relatively easy to genetically manipulate the traits thereby increasing the chance of success in breeding for higher photosynthesis.

In perennial fruit trees, storage of assimilates play an important role in the interaction between current and subsequent growth cycles (Monselise and

Goldschmidt, 1982). The normal growth, development and productivity of plant depend on the availability of stored foods and availability of current photosynthates. The partitioning of assimilates to different vegetative and reproductive organs during various stages of development of lateral give vital clues on the physiological processes determining productivity. Such information will provide the basic data needed to develop crop management strategies, crop growth models and future breeding strategies.

In recent years, physiological and biochemical parameters are being used as markers for early evaluation of progenies. A better knowledge about the physiological and biochemical constituents among different genotypes and their contribution to yield and yield attributes is thus helpful in formulating early selection criteria in progenies. A detailed study on the pattern of vegetative growth and constituents of metabolites in the leaves that may influence berry growth, development and yield assume significance in this context.

A deep insight into the role of various physiological and biochemical factors that determine productivity in black pepper is still lacking and the information available on these aspects are meagre. The growth and yield parameters also are not clearly defined. Information is scanty on the photosynthetic efficiency and translocation pattern of metabolites in black pepper.

In the light of the above facts, the investigations reported herein were undertaken with the following objectives:

To elucidate the chronological events and processes that take place in the plagiotropes of black pepper starting from flushing to harvest of spike.

To determine the important growth and yield parameters, pattern of dry matter production, distribution and partitioning in the plagiotropes of black pepper genotypes.

To assess the photosynthetic efficiency and translocation at different growth and reproductive stages of the crop, employing radiotracer technique.

To correlate the influence of morphological, photosynthetic and biochemical parameters with yield and to assess the contribution of these traits towards productivity in black pepper.

Review of literature

REVIEW OF LITERATURE

Analysis of morphological, physiological and biochemical variation among the genotypes with respect to their productivity assume significance for screening in plant improvement programmes. Information on the physiological and biochemical aspects of flowering is limited and unclear in black pepper and it is difficult to find out the cause and effect. This is perhaps due to the fact that majority of the workers have assessed the different aspects of this problem in isolation rather than in its totality. In view of this, relevant studies related to the growth pattern, flowering, fruit-set, and physiological and biochemical parameters, photosynthesis, dry matter accumulation and partitioning that influence yield in black pepper are reviewed in the following pages. Since much information is scanty in black pepper, work carried out in other important crops of relevance are also incorporated.

2.1 Climate and black pepper

In several tropical tree crops, flowering is often induced by rainfall (Alvim, 1964). Borchert (1983) had shown that flowering in some tropical trees occur in response to decreased water stress, which may be stimulated either by leaf loss or rainfall.

According to Nalini (1983), rainfall was the most important factor influencing flower bud differentiation in black pepper. Receipt of pre-monsoon showers after the dry spell during December to April triggered the flower bud differentiation activity in this crop. She had also reported that hours of sunshine were negatively correlated with the flower bud differentiation. Rajan (1985) also had emphasised the importance of rainfall in flowering of black pepper. He reported that maximum and minimum temperature in the preceding summer and the subsequent monsoon showers played important role in triggering the flower bud differentiation activity. These factors exhibited significant positive correlation with the process. Humidity showed positive correlation at the time of differentiation while sunshine hours recorded negative correlation. Pillai *et al.* (1987) investigated the rainfall pattern and pepper yield during the two extremely adverse years (1980-81 and 1986-87) in which there was a distinct break in the rainfall during critical period following flower initiation. The break was experienced at two different periods and therefore at different stages of the crop during the two years. The rainfall was compared to that of the favourable year (1981-82). In both the adverse years, it was found that pepper yield was as low as 24.3 per cent of the normal year's yield. On the contrary, during the favourable year, precipitation remained steady without any break and pepper yield was high. This indicated that a break in the rainfall even for a period of few days at a stretch occurring during any part of the critical period of the reproductive phase of pepper plant would affect the yield considerably.

Wide differences have been reported among varieties in their response to intensities of shade and light. Nambiar (1978) had observed that the light requirement of Panniyur 1 was more than the local varieties like Kalluvally and Karimunda and shade encourage vegetative growth in this variety. Shade also reduces fruit set in pepper in general (Ramadasan, 1987). According to Mathai and Sastry (1988), higher light availability during pre -flowering (March- April) produced greater leaf area and more compact canopy structure with shorter lateral shoots. This allowed the vine to accumulate higher level of metabolites, which lead to greater production of lateral shoots, flowers, spikes and berries per vine and higher dry matter content of berries. The vines under high light regime were seen to produce more number of berries per unit surface area while it was low under low light regime. But irrespective of conductance, Panniyur 1 produced more number of berries per unit surface area than Karimunda.

2.2 Growth studies

Growth analysis is an important tool in investigating the productivity aspects of crop plants. Various systems are adopted for identifying the various growth phases during the phenological development of tree crops (Challa, 1988 and Challa, 1997).

The tree crops in general bear crop either on the past season's growth or current season's flushes. Therefore any natural factor, which serves to promote the growth, may be responsible for promoting yield (Acock and Reynolds, 1989). Various factors like morphological and physiological parameters, previous year's crop load etc., have been reported to influence the phenomenon of vegetative growth and fruit-bud differentiation.

2.2.1. Flushing and shoot growth

In black pepper variety Panniyur 1, Menon (1981) observed that shoot growth started during late May and continued to mid August with maximum growth occurring in June. The maximum extension growth of the laterals occurred in July (46.7%) followed by June (35.73%), May (4.36%) and August (3.47%). The percentage of laterals that showed extension growth also followed the same trend. Kurien and Nair (1988) observed two growth flushes in black pepper, one in May and the other during October-November. Histological studies carried out by Nalini (1983) in laterals revealed that differentiation of vegetative buds was observed throughout the season. Maximum differentiation of vegetative buds occurred during June-July (40.0 to 67.5%) and minimum during January to March (5.0 to15.0%). Maximum extension growth (80.0 %) of laterals occurred during the months of June –July while the growth was minimum (2.0 %) during the month of February and March. The extension growth of shoots varied between 5.28 cm and 12.04 cm with a mean of 10.27 cm in a year.

Rao and Sebastian (1994) derived constants for computing leaf area in black pepper using the portable leaf area meter, LI 3000 A. The leaf area was estimated using two simple linear regression equations, Y= a + bx and Y= bx and the latter was found to be the best. As the equation Y= bx had overall superiority, the equation could be used for estimating leaf area in black pepper. The leaf area is arrived at, as a product of length and maximum width of the leaf multiplied by the constant, 0.70.

Five cultivars of black pepper were evaluated for 8 growth and 11 yield attributes at harvest by Mathai *et al.* (1991). Vines with smaller leaves, shorter internodes, vigorous branching and smaller canopy surface received increased sun light penetration and air movement within the canopy. Such condition reduced the number of lateral branches but increased the number of productive laterals and number of spikes on each lateral.

In cashew, Rao and Hassan (1957) reported two active growth phases, one beginning in October and lasting till January and another between March and May. Of these two phases shoots produced during October- January gave rise to panicles while the flushes emerged later were invariably unproductive. Damodaran *et al.* (1965) stated that the main season of cashew flowering was October – November, which commenced by the middle of September and continued until the end of February under Kerala conditions. Hallad (1991) observed that most of the cultivars produced new flush from second fortnight of October to the end of November at Dharwad. Pushpalatha (2000) reported that the period of flushing and flowering in cashew varied among the accessions and majority of them started flowering during November- December.

In mango, vegetative growth and flowering is said to be an annual feature in certain varieties which are acclaimed as 'regular bearers' (Singh, 1960). In alternate bearing varieties, bienniality is observed both in flowering and vegetative growth. Such varieties have been observed to produce flowers in 'on' year and vegetative growth in 'off' year implying that some kind of antagonism between vegetative growth and reproductive growth may exist in mango (Pandey, 1988).

Hittalmani *et al.* (1977) studied the main growth and flowering seasons of Kagzi lime and Tahiti lime. The seasons were December-January and May-July for Kagzi lime and Tahiti lime respectively.

Ojha *et al.* (1985) studied the flowering behaviour and growth pattern of guava cultivars Sardar and Allahabad Safeda and reported that they flowered twice in a year, during April – May and July – August. Flowering duration was greater in rainy season (July - August) compared to the season from April – May. They observed two growth flushes, one during January – February and the other during June.

In coffee, the pattern of shoot growth under South Indian condition is typically sigmoidal in nature with a period of slow growth from March to July and a period of rapid growth from August to October. After October, the growth will slow down due to low moisture content of soil and ripening of fruits (Vasudeva and Ramaiah, 1979 and Ramaiah and Venkataraman, 1985). There is an antagonistic effect existing between vegetative and reproductive growth.

2.2.2 Leaf growth and development

The leaf lamina is the major photosynthetic organ of the plant to intercept sun light and the productivity of the plant directly depends on the chlorophyll bearing surface area, irradiance and its potential to utilise carbon dioxide (Wahid *et al.,* 1997). Leaf area is an important parameter, which governs fruit growth and maturity in several fruit crops. Evidences suggest that leaf production, leaf area index, leaf orientation and other factors have major influence on radiation harvesting processes.

Geetha (1990) and Geetha and Aravindakshan (1993) observed that the number of leaves, total leaf area as well as biomass production differed significantly between vine and bush pepper.

A numerical index, the Leaf Plastochron Index (LPI) was developed to study leaf development. A plastochron is the period of time between initiation of successive leaf primordia at the shoot apex of a higher plant or the interval between corresponding stages of development of successive leaves. Plant development stage is usually expressed as plastochron index (Heuvelink, 1995). Schultz *et al.* (1996) investigated the relationship of photosynthesis to leaf age and tested suitability of plastochron index concept for the description of age related changes in leaf photosynthetic activity in grapes. The results indicated that plastochron is an adequate indicator of time as experienced by the plant and is superior to the thermal time (degree-day) and other chronological time expressions commonly used to relate photosynthesis to development.

In grape cv. Italia, Kingston and Epenhuijesen (1989) found that for optimum ripening and more berry weight, leaf area of 7.2 cm^2 and 9.5 cm^2 respectively was required. The optimum leaf number per shoot was 11 for large berry size and 13 for early ripening. Jianhua *et al.* (1996) had reported that in grapes cv. Kyoho, leaves showed a single sigmoid pattern of growth. The period of rapid growth lasted for 7 to 9 days while the period of expansion for a single leaf lasted for 15 to 32 days.

In coffee, leaf growth showed a periodicity as observed in shoot growth. The initiation of leaves was higher during August-September and the area of these leaves was also high. The life span of coffee leaves ranged from 40-50 days (Vasudeva and Gopal, 1975).

2.3 Flowering, spike growth and development

Black pepper being an evergreen perennial crop, its pattern of vegetative and reproductive growth is controlled by a combination of physiological, biochemical and environmental factors. With the onset of monsoon, new leaves start emerging from the previous season shoots. From the axil of new leaves, spikes are initiated. These are emerged covered in sheaths. The colour of the sheaths varies from green to pink or even violet. It takes 20 to 25 days for the full emergence of spikes from sheaths. After the emergence of spike, the flowers start opening between 8-14 days and progressively advance towards the tip. It may require 6-9 days for the complete opening of the flowers on a spike. The laterals continue to grow and in the axil of the new leaves formed, fresh spikes may be developed (Chandy *et al.*, 1984). Menon (1981) reported that flowering was confined to 4 months from May and followed a pattern similar to the growth of shoots with maximum in July (50.33 %) followed by those in June (29.62 %), May (11.80 %) and August (8.46 %). Significant variation existed between standards with respect to the percentage of flowering. Nalini (1983) reported a spurt in flower bud differentiation activity immediately after the receipt of pre-monsoon showers. Maximum flower bud differentiation occurred in June–July (40.0 - 95.0 %) and the process of flower bud differentiation was completed within 20 days of commencement. Rajan (1985) reported that maximum flower bud differentiation was observed from the middle of June to the end of July in Panniyur 1. The peak appeared to be a little advanced in Karimunda, from the beginning of June to the middle of July. Compared to Panniyur 1, Karimunda showed fair amount of flower bud differentiation during some of the other months also. The process of differentiation was completed within 25 days of initiation.

Nambiar *et al.* (1978) reported that most of the high yielding and popular cultivars produced 70-98 per cent hermaphrodite flowers. The percentage of male flowers in a spike varied from 0-19 while bisexual flowers showed a wide variation from 2-93 per cent. They also found that the proportion of female flowers increased with an increase in the intensity of shade. Off-season spikes produced were characterised by more number of female flowers than those produced in the normal flowering season. Menon (1981) found that the mean number of flowers per spike were 107.74, with 97.18 per cent hermaphrodite and 2.82 per cent pistillate flowers. In Karimunda, the spikes had a mean of 46.23 flowers, which were all hermaphrodite.

Spike length is another character of importance, which controls the yield in pepper along with increased fruit set. The spike development followed a linear pattern. Spike length varied between 5.9 cm to 13.4 cm in 18 varieties studied (Nambiar *et al.*, 1978). In Karimunda, the maximum length (6.20 cm) was attained in 29.26 days while in Panniyur I, 31.67 days were required to attain the maximum length (12.5 cm) (Menon, 1981).

The period of anthesis in a spike varied from 6-10 days (means 8.12 days) in Panniyur 1 and 4 to 11 days (mean 9.21 days) in Karimunda. The anthesis of flowers commenced on 17.33 days after emergence of spike in Panniyur 1 and was completed in 25.44 days. In Karimunda, anthesis started 19.01 days after emergence and was completed in 28.22 days (Kanakamani, 1982).

According to Chandy *et al.* (1978), every new leaf produced has the potential to initiate spike in its axil. But majority of these spikes may either be aborted or shed within 6-7 days after spike emergence. The percentage of abortive spikes ranged from 17.4 to 86.2 among the varieties. The percentage of abortive spikes in Panniyur 1 and Karimunda were 32.3 and 37.5 respectively. Pillai *et al.* (1977) have observed varietal differences in spike shedding. Average shedding percentage of spikes varied between 14.0 to 65.0 per cent among genotypes. Varieties Kalluvally, Karimunda and Panniyur 1 showed 14.0, 21.9 and 26.2 percent shedding of spikes respectively. Shedding differed very much between seasons. In addition to varietal differences, spike drop in pepper has been observed to be more in shade grown plants. Shedding of spike was also influenced by environmental factors. Apart from the shedding during initial stages, another wave of intensive shedding of spikes occurs during the advanced stages of berry development. This is said to be due to the physiological disturbance in plant (Pillai *et al.*, 1977). Spike shedding was observed in almost all the months starting from spike emergence till harvest. Maximum (51.31 %) was noticed in June and minimum in May (1.69 %). There was no shedding in September. Spikes were shed at various stages of development, starting from emergence to harvest. Maximum shedding (33.15 %) was observed during first month of berry set followed by those stages before anthesis (24.86 %) and during anthesis (16.57 %) (Menon, 1981).

Cashew plants normally started flowering from third year of planting. The growth pattern of bearing trees consists of a vegetative flush and a generative flower flush. Flowering was terminal and was universally preceded by the vegetative flush (Rao and Hassan, 1957). Season of flowering was reported to differ from region to region and was attributed to variation in the climatic condition (Dasarathi, 1958., Damodaran *et al.*, 1965., Gowda *et al.*, 1986, and Hallad, 1991).

In cashew inflorescence, the unproductive staminate flowers outnumber the productive hermaphrodite flowers and several workers have reported significant and positive relationship between proportion of hermaphrodite flowers and yields (Rao and Hassan, 1957., Aiyadurai and Koyamu, 1957., Damodaran *et al.*, 1965., Pavithran and Ravindranathan, 1974 ., Chakraborthy *et al.*, 1981 and Pushpalatha, 2000). The number and percentage of hermaphrodite and staminate flowers also varied according to the growth flushes and regions (Pavithran and Ravindranathan, 1974., Pillai and Pillai, 1975., Hanamashetti *et al.*, 1986 and Hallad, 1991).

In mango, Rao and Bhandary (1975) recorded the sex ratio and percentage of hermaphrodite flowers as 27.10 and 3.57 per cent and 26.10 and 3.84 per cent respectively for Alphonso and Pairi.

2.4 Fruit set and development

Pollination and fertilisation are two important pre-requisites for fruit set and development in any fruit crop. If these do not take place properly the ovary usually fails to enlarge and set fruit. The growth of the fruit involves the enlargement of the ovary and the associated parts.

Fruits exhibit mainly two types of growth patterns. Some fruits exhibit sigmoid type of growth whereas several other fruits exhibit double sigmoid pattern of fruit growth and the growth pattern to vary with species, variety and climate (Leopold, 1964).

Berry development in black pepper starts soon after anthesis and it requires about 150 days for complete maturity. Shade was found to influence spike formation and berry setting in pepper vine. Generally all the hermaphrodite flowers will not develop into berries of normal size and this depends on the availability of photosynthates. The berries, which fail to develop into normal size, will stop their development at various stages of growth. These are referred to as undeveloped berries or light berries (Chandy *et al.*, 1978).

Karianchen and Deve (1989) studied the anatomical, histological and biochemical changes in the berries of black pepper during ripening. Rathnawathie (1984) observed the effect of berry maturation on some chemical constituents of black, green and white pepper. Starch content increased (Jansz *et al.*, 1984 and Pruthi, 1993) while crude fibre and moisture decreased (Sumathikutty *et al.*, 1989 and Pruthi, 1993) at later stages of berry maturation.

In cashew under natural conditions, fruit set was found to vary from variety to variety and percentage of fruit set was found to be very low (Rao and Hassan, 1957., Damodaran *et al.*, 1965 and Pushpalatha, 2000).The fruit set was also found to vary from region to region (Rao and Hassan, 1957., Dasarathi, 1958., Damodaran *et al.*, 1965 and Damodaran, 1966., Pillai and Pillai, 1975., Parameshwaran *et al.*, 1984., and Gowda *et al.*, 1989).

Singh (1964) stated that the initial fruit set in mango was largely dependent on the extent of hermaphrodite flowers produced. Singh *et al.* (1966) observed a higher fruit set and better retention of fruits per panicle in the medium and late emerged panicles compared with the early-emerged panicles.

In pomegranate, a gradual increase in length and diameter of fruit was recorded through out the period of development indicating a sigmoidal type of growth pattern (Nanda, 1996).

Hittalmani *et al.* (1977) suggested that the Kagzi lime fruit followed a sigmoid pattern of growth and took 6 ½ months to mature from the time of fruit set. The growth pattern could be divided into 3 distinct periods based on the rate of growth. The period I being the period of rapid growth from first to fourth fortnight, period II being the stage of steady increase in weight from fifth to ninth fortnight and period III marked by an accelerated growth rate from tenth to thirteenth fortnight. The specific gravity of the Kagzi lime fruit showed a declining trend from fruit set to maturity.

Damodaran (1966) observed the development of cashew nuts at different stages of their development and found that the length and breadth of nuts at 8th week after fruit set was 26 mm and 17 mm, respectively. Ohler (1977) observed a great variation in the size of nuts in Brazil where the largest nut was 53 mm and weighed over 15 g. The length of the smallest nut was 18 mm, which weighed little over one gram.

Growth of fruits in sapota, showed a double sigmoid nature of growth and required about 10 months for full development of the fruits (Mitra, 1999).

Growth of grape berry followed a double sigmoid curve with the 3 distinct growth phases. The two active phases are divided by a period of slow growth known as lag phase. Most of the cell divisions and development of seed in the berry occur in the first period of rapid growth (Coombe, 1973).

Growth curves of arabica coffee fruits showed a bi-sigmoidal shape (Ramaiah and Vasudeva, 1969). Under south Indian condition, the berry growth is minimal up to 42 days after flower opening and then increased rapidly up to 102 days. A drop in the fresh weight between 102 and 117 days was followed by another steep rise up to 212 days and then cessation of berry growth. The dry weight accumulation of the berry as a whole or endosperm was similar to that of berry. The dry weight accumulation of the berry as a whole or endosperm showed a bi-sigmoidal pattern. Three periods of dry weight accumulation in coffee berries could be identified. The first slow phase between 42-117 after anthesis, the second growth phase between 117-152 days and third and final grand phase from 182 days onwards (Ramaiah and Venkataramanan, 1985).

2.5 Assimilate production and biomass partitioning

In perennial tree crops generally, yield depends on the balance between the vegetative and reproductive growth. Production is affected by the distribution of translocated carbon to new leaf and shoot growth and by the accumulation of carbon in harvestable organs. The former affects assimilate production while the latter affects harvest index. As a consequence, increased plant productivity requires a balanced increase in the source carbon that is partitioned to these two sites (Gifford and Evans, 1981 and Patric, 1988). As such, one of the requirements for analysing plant productivity is the availability of accurate data in assimilatory organs like the leaf and the accumulation of dry weight by the plant and its economic parts.

Among the five black pepper cultivars studied, Mathai and Nair (1990) observed that Panniyur 1 produced more laterals, spike and berries than other cultivars and have higher mean berry weight. Varieties showed variability in their productivity levels. Varieties with large structural growth in general were found to yield less and variety Karimunda having a smaller vegetative structure has been found to be highly productive. Mathai *et al.* (1988*)* reported that the current season growth in the lateral shoots generally bear the economic sink. Hence the pattern of partitioning of dry matter among various organs of these structures decides the ultimate productivity of the vine. Internodes, spikes and leaves are the main organs of these laterals. The relationships existing among leaves, spikes and internodes of a lateral with regard to dry matter distribution has been studied. It was observed that during early stages of spike development, the demand for current photosynthates was comparatively less in the productive laterals of black pepper (58. 8 %). However, this demand went up to about 97 per cent towards advanced spike development stage. At this stage, while the older spikes received 37.63 per cent of the metabolites, the younger ones got only 25.71 per cent. This was due to the increased sink activity during this period of growth and hence any factor detrimental to the source activity during the stage can affect the final filling of berry and yield. Mathai and Nair (1990) reported that specific leaf weight was higher in Karimunda than Panniyur 1. They obtained positive and significant relationship between biomass production and economic yield within laterals. They also noticed maximum biomass in leaves than stem in all the cultivars. Geetha and Aravindakshan (1993) observed that the number of leaves, total leaf area as well as biomass production differed significantly between vine and bush pepper and were dependent on nitrogen levels.

Experiments were conducted at Indian Institute of Spices Research, Calicut, by Krishnamurthy *et al.* (2000) to investigate whether the developing spike was completely dependent on the subtending leaf for its nourishment in black pepper. The treatment consisted of 25, 50 and 100 per cent leaf removal and no leaf removal. Spike weight and berry set percentage differed significantly among treatments. Total carbohydrate content of leaves decreased while it showed an increase in the subtending berries in all the treatments and control especially during later stages of spike development. Leaf protein increased while berry proteins decreased and nitrate reductase activity showed a reverse trend. The results indicated that the developing berries may not be fully dependant on the subtending leaf for their nutrients which was supported by fruit set percentage (80.0 % fruit set under 75.0 % leaf removal treatment as against no leaf removal).

In grapes, reports indicated that there is a positive correlation between import of sugars in sink organs in relation to sink strength (Ho, 1988). Leaf area was inversely related to crop load, with differences evident as early as fruit set. Leaf and shoot dry weights were inversely correlated and fruit dry weight was positively correlated with crop load. Root dry weight was inversely correlated with crop load, only at harvest. Leaf area per vine, leaf size, shoot length, number of nodes and internodal length were inversely related to crop load. Fruit number per cluster and cluster weight was inversely correlated with cluster number per vine (Edson *et al.*, 1995 a). Fournioux (1997) observed that flowering was the critical deciding point as far as the assimilates were concerned. Before flowering, vegetative growth was predominant over reproductive growth, but after fruit set, the grape bunches had the advantage. When there was competition for reserves, vegetative growth was a greater sink than bunches until the start of ripening.

Chacko and Ananthanarayanan (1982) studied the relationship among leaf number, leaf area and fruit development in mango. The optimum leaf number to fruit ratio in various mango cultivars was sought by isolating individual fruits with known numbers supporting leaves by shoot girdling.

In coffee, observations made for two seasons on leaf to fruit ratio of *C. arabica* cv. S. 795 and *C. canephora* cv. S. 274 revealed that the leaf to fruit ratio was varying from season to season depending on berry drop and defoliation. It also revealed that 17.70 cm^2 of leaf area was required to support one fruit in case of arabica and 5.0 cm^2 for robusta. But majority of the nodes carried only 1 to 5 fruits in arabica and 11 to 20 on robusta. The cropping branches of arabica and robusta plants were 52 and 61 respectively (Vasudeva and Ratageri, 1981). Coffee leaves initiated in August- September had higher dry weight, apparent photosynthesis and nitrate reductase activities (Venkataramanan, 1985).

2.6 Carbohydrte /Nitrogen accumulation and flowering

Nalini (1983) reported that in black pepper, total soluble carbohydrate, nitrogen and C/N ratio of the new shoot growth varied considerably during the growth cycle. Carbon/nitrogen ratio exhibited two peaks, the first synchronising with the commencement of differentiation process and the second with the stepping up of flower bud differentiation activity. Rajan (1985) reported that carbohydrate accumulation and C/N ratio build up were obtained prior to the peak flower bud differentiation period. However carbohydrate content and the C/N ratio failed to show significant correlation with flower bud differentiation. High nitrogen content in the leaves and stem of black pepper was observed during the month of June (Nybe *et al.,* 1989).

Aruthyunyan (1977) noted that flower bud initiation and differentiation in apple coincided with high leaf carbohydrate contents, especially starch. Kandaih, (1979) observed seasonal changes in carbohydrate content in all parts of apple trees, characterised by depletion during spring with the beginning of more shoot growth and replenishment later. Yoshioka *et al.* (1988) reported that trees of cv. Jonagold accumulated starch in the roots and branches as reserve carbohydrates in summer, and in winter, this was changed to soluble carbohydrates such as glucose, fructose and sucrose.

In cashew, Ankaiah and Rao (1983) observed that chlorophyll and starch contents of mature cashew leaves would give a fair indication of the bearing capacity. The average chlorophyll and starch contents in leaves of high yielder and low yielder were 9.83 and 7.90 per cent for chlorophyll and 7.19 and 6.90 per cent for starch respectively. Suryanarayana (1987) reported that

Carbohydrate/nitrogen ratio decreased with the increase in the age of shoots. Maximum C/N ratio was recorded in four month old shoots and lowest in six months old shoots.

Many evidences are available which show that citrus trees used both reserve and currently produced carbohydrates, resulting in marked depletion of these reserve (Hilgeman *et al.*, 1967 and Sanz *et al.*, 1987). In grapes, Antcliff and Webster (1955) related the influence of carbohydrates and their fluctuations on the process of initiation and differentiation of flower buds. Accumulation of carbohydrates promoted initiation, differentiation and consequently resulted in clusters. A reduction of this constituent on the other hand reduced the formation of clusters. Melanta (1967) studied the chemical changes of the developing grape buds of Anab-e-Shahi and found that the C/N ratio was minimum on the 39th day after bud burst while it was higher on the 67th day followed by slight modifications on the 74th day. Rao and Sathyanarayana (1978) reported that when grape vines were pruned to two buds and the growing shoots were analysed at 10 days interval from 40th to 160th day after pruning, the shoot carbohydrate and nitrogen contents were maximum during the fruit-bud initiation period. A demographic model on assimilation and allocation of carbon and nitrogen in relation to flowering and fruiting in grapevines were reported (Wermelinger *et al.*, 1991).

In mango, Singh (1960) and Veera and Rao (1977) reported that higher contents of starch, total carbohydrates and C/N ratio favoured flower bud formation and fruit bud differentiation. Organic nitrogen did not appear to have any direct bearing on fruit bud differentiation. Sen *et al.* (1965) noticed a significantly high C/N ratio in the bark during fruit-bud initiation and differentiation period. There was rise in the carbohydrate content of shoots from November to January. In the cultivars Langra and Himasagar, flowering shoots contained higher levels of total sugar, carbohydrate and soluble nitrogen than non-flowering shoots. Chacko and Ananthanarayanan (1982) analysed the bark at the time of flower bud initiation and observed greater accumulation of carbohydrates particularly sucrose.

Carbohydrate reserves of coffee plants would affect fruit growth (Cooil and Nakayama, 1953). Fruits continued to grow even after complete depletion of starch from the wood and then from the leaves (Wormer and Egabole, 1965). Developing fruits could also utilise starch from the wood and leaves (Patel, 1970). Janardhan *et al.* (1971) and Gopal *et al.* (1975) studied the carbohydrate reserves in S. 795 arabica coffee plants and found that wood starch played an important role in the formation and development of flower buds and their successful opening.

2.7 Photosynthesis

Photosynthesis is the only source for biomass accumulation. There is a direct correlation between biomass and crop yield. Approximately 90 per cent of plants dry weight originates from products fixed in photosynthesis. So photosynthesis form the subject of many studies which is sought to understand the variation in plant growth and productivity (Poorter *et al.*, 1990).

Leaf photosynthesis showed a close positive relationship with yield in grapes under field conditions (Edson, 1991). There have been instances in which a good correlation between leaf photosynthetic rate and yield has been reported in various tree species (Muthuchellian, 1992). Photosynthesis was positively associated with crop yield in asparagus and photosynthetic rate may be used a predictor of yield and is of potential use in early selection for breeding (Faville *et al.*, 1999). Bai and Kelly (1999) observed that variability in photosynthetic capacity was correlated positively with the long-term economic yields of asparagus genotypes. Genotypes having high photosynthetic rates were found to have high specific leaf mass. Selecting for high specific leaf mass could be adopted as a method for preliminary selection of genotypes with high photosynthesis rates.

2.7.1 Genotypic variation and photosynthesis

A considerable degree of genetic variability in photosynthetic rate per unit leaf area has been shown in a number of crops (Dejong, 1983., Sheshshayee, 1992 and Muthuchelian, 1992) and among genotypes (Ananthakumar, 1982) . Variability among genotypes in photosynthetic rate were reported in grapes (Schubert *et al.*, 1996), cashew (Latha, 1998), soybean and sunflower (Krishnaprasad, 1994) and asparagus (Bai and Kelly, 1999).

2.7.2 Factors regulating assimilation rate

It has been clearly established that various endogenous and environmental variables impose a certain degree of regulation to the process of photosynthesis either by their effect on stomatal or mesophyll factors.

2.7.2.1 Crop load

In grapes, Wen and Liu (1989) observed that leaves on fruiting shoots had higher photosynthetic rate than those on non-bearing shoots. Albuquerque and Regima (1995) investigated the effects of cluster removal on photosynthesis and stomatal conductance at three stages of fruit maturation in grapes. Photosynthesis and stomatal conductance was similar in plants with or without cluster removal, but in high yielding cv. Ugni blane photosynthetic activity and stomatal conductance was significantly higher in fruit bearing plants than in plants with the clusters removed. Edson *et al.* (1995 b) reported that single leaf photosynthesis was positively correlated with crop load in each developmental stage. Whole vine photosynthesis was positively correlated with crop load only at harvest. Whole vine photosynthesis was inversely correlated with crop load at mid season, indicating that vegetative and fruiting sinks strongly influence whole vine photosynthetic rates in grapes.

2.7.2.2 Leaf characters

An inverse relationship between individual leaf size and photosynthesis has been reported. Photosynthetic rate expressed on leaf area basis showed positive correlation with relative growth rate in 24 wild species studied (Poorter *et al.*, 1990).

Intrieri *et al.* (1992) investigated the influence of leaf age and leaf position on photosynthesis in grapes. Maximum photosynthetic rate was observed at about full leaf expansion (35-40 days of age) and a decline thereafter. But leaves older than 4 months maintained 70 per cent of their maximum assimilation rate. However, Schubert *et al.* (1996) reported that net photosynthesis of field grown plants reached a maximum in 20-40 day old leaves. At lower light intensity (150 µ moles m^{-2} s^{-1}) photosynthesis reached a maximum in 50-60 day old leaves. In grapes cv. Kyoho, Jianhua *et al.* (1996) had reported that the highest rate of net photosynthesis was achieved by leaves that were fully expanded at flowering. Schultz et al. (1996) investigated the relationship between insertional level of leaf and photosynthesis (A) of grapevine cv. White Riesling. Lateral leaves had the highest rate of CO_2 assimilation and carboxylation efficiency. In three year old potted *Vitis vinefera* cv. Freisa plants, Lovisolo *et al.* (1997) observed that net photosynthesis was lowest both in young and old leaves at high as well as low light intensity. These leaves also had a lower stomatal conductance. Shiraishi, *et al.* (1997 a) reported that in grapes, there was no correlation between photosynthetic parameters and leaf shape.

Palanisamy and Yadukumar (1993) reported that in field grown cashew trees, maximum net photosynthetic rate was found in the leaves of middle portion of the tree.

Photosynthesis and assimilate partitioning during rhythmic growth in tea was investigated by Botwright *et al.* (1998). Photosynthetic capacity and the pattern of carbohydrate partitioning varied during shoot growth at various stages of development. Net photosynthesis was highest (18.0 µmol CO_2 $m^{-2}s^{-1}$) at the beginning of shoot growth and lowest (13.2 µmol CO_2 $m^{-2}s^{-1}$) at the cessation of shoot extension.

The effect of leaf age and environmental effects on gas exchange in leaves of banana was investigated by Thomas and Turner (1998). Net photosynthetic rate reached a maximum of 20-25 µmol CO_2 $m^{-2}s^{-1}$, 9 day after the leaf had unrolled, when another new leaf had emerged and the measured leaf was in the second leaf position.

2.7.2.3 Photosynthesis and stomatal conductance

Occurrence of a positive correlation between photosynthetic rate (A) and stomatal conductance (g_s) was observed among various species and among different physiological treatments. When the g_s is lower, the capacity of assimilation also tends to be lower (Wong *et al.*, 1978). Ehleringer and Bjorkman (1978) suggested that stomatal conductance is related to photosynthetic rate of crop plants.

Yem *et al.* (1998) investigated the relationship between photosynthesis and changes in microclimate in ginger. Stomatal conductance (g_s) increased rapidly as irradiance increased and was saturated at relatively low light intensity (400 μmol CO_2 $m^{-2}s^{-1}$). Transpiration increased with increasing irradiance and temperature. Increasing external CO_2 concentration caused a reduction in stomatal conductance and transpiration rates. Stomatal conductance was relatively insensitive to increasing soil moisture availability until a threshold was reached with increasing transpiration.

2.7.2.4 Photosynthetic rate and intercellular CO_2 concentration

Several studies support an increase in 'A' with increase in internal carbon dioxide concentration (Ci) (Caemerer and Farquhar, 1981., Campbell *et al.*, 1988 and Krishnaprasad, 1994). The exact increase in 'A' with increase in intercellular CO_2 varies among species and with other environmental factors. But it is essentially the same for many C3 species. A mere doubling of Ci had been shown to increase A at a given light intensity though the range varies from 20 to 300 per cent (Sage *et al.*, 1989).

2.7.2.5 Light response to photosynthesis

The response of photosynthesis to light (A/ light response) at different CO_2 levels were studied in 5 coastal desert plant species (two C4 species and three C3 species) and five tropical rain forest plant species (all C3 species) using L1-6400 portable photosynthesis system. The A/light response curves in intact leaves of different species under a series of CO_2 concentrations (350-1500 μmol mol^{-1}) were measured. When CO_2 concentrations were elevated, the light saturation point (LSP) and light compensation point (LCP) increased for most C3 species, especially the LSP. But for the C4 species, changes in LCP and LSP were small (Naidu and Swamy, 1995).

Pathirathna *et al.* (1998) investigated the effect of shade on photosynthesis of cinnamon leaves. Photosynthetic rate at light saturation increased from 5.14 to 7.25 μ moles m^{-2} s^{-1} as growth irradiance increased from 12-100 per cent day light.

Eight *Vitis* species and 6 cultivars were studied for the relationship between photosynthetic activity and light intensity (Shiraishi *et al.*, 1997 a). Photosynthetic rate of leaves increased with the level of light intensity. Transpiration rate and stomatal conductance increased linearly with light intensity and thereafter increased progressively. Intercellular CO_2 concentration decreased with increase in light intensity

2.7.2.6 Temperature response to photosynthesis

The variation in photosynthesis in response to variation in atmospheric temperature has been reported in various C3 and C4 plants (Ehleringer and Bjorkman, 1978). Shiraishi *et al.* (1997 b) investigated the effects of temperature on photosynthetic rate and various other physiological parameters. Six species of *Vitis* were evaluated for photosynthetic parameters at 15-35 ^{0} C. Highest photosynthetic rate was reached at 20-30 ^{0} C, the optimum varying with species. Transpiration rate increased with intercellular CO_2 and water use efficiency reached their respective maxima at 15-20 ^{0} C.

Xizhen *et al.* (1998 a) reported that ginger leaves showed the highest photosynthetic rate and apparent quantum efficiency at 25^0 C. Photosynthetic rate increased with increasing light intensity and CO_2 concentration. The light compensation point was in the range 25-69 µmol CO_2 $m^{-2}s^{-1}$ and increased with the increase in temperature. Photosynthesis was saturated at a light intensity of 642-867 µmol $m^{-2}s^{-1}$, which depended on temperature above or below 25^0 C. CO_2 compensation and saturation points increased with increasing leaf temperature.

2.7.2.7 Water stress and photosynthesis

Plants suffering from severe drought and chilling stress show little or negative photosynthetic CO_2 assimilation rate (A) when measured at light intensities that saturate photosynthesis in unstressed plants. Nevryanskaya (1989) studied photosynthesis in some grape varieties under different moisture regimes. Moisture stress reduced photosynthetic rate, specific leaf weight, leaf area and dry matter accumulation in the leaves. Shishkanu *et al.* (1992) studied the photosynthetic activity of grapevine shoots under different water availability and found that a decrease in soil moisture level generally resulted in marked decrease in photosynthetic activity.

2.7.2.8 Photosynthesis and vapour pressure deficit (VPD)

Vapour pressure deficit affects the photosynthesis by altering the stomatal conductance. Increased vapour pressure deficit is mainly caused by an increase in air temperature (Allen *et al.*, 1990). An increase in air temperature caused an increase in canopy transpiration and reduced the stomatal conductance as a result of higher VPD (Jones *et al.*, 1985). The effects of moisture regimes on carbon exchange parameters have been studied by Gurumurthy (1994) in *Eucalyptus* and *Dalbergia sissoo.*

2.7.2.9 Photosynthetic studies in black pepper

Chanzdon and Field (1987) investigated photosynthetic capacity in six pepper species. Mathai *et al.* (1988) reported that black pepper variety Panniyur 1 translocated higher percentage of photosynthates to the developing spike during berry development and recorded higher photosynthetic rate resulting in higher yield than other cultivars. They also observed that 45 days old pepper berries depend more on stored photosynthates while berries older than 45 days depend more or current photosynthates for its dry matter accumulation. He explained the reduction in the yield attributes to reduced availability of current photosynthates.

Influence of source area on photosynthetic accumulation and yield attributes in laterals was investigated by Mathai *et al.* (1989). The lower leaves were removed from selected laterals after 60 days of spike initiation in variety Panniyur 1, reducing the average source size (leaf area) by an average of 62 per cent. This severe limitation of area for the production of current photosynthates reduced further extension of spike length by 18 per cent, the number of normally developed berries per spike by 39 per cent and individual berry dry weight by 22 per cent. These reductions were considerably less than the reductions in leaf area, suggesting partial compensatory mechanism in photosynthesis. Krishnamurthy *et al.* (2000) investigated the influence of water stress on some physiological parameters in black pepper germplasm accessions. Stomatal resistance, free amino acids and reducing sugars increased while transpiration rate and protein contents decreased with an increase in stress intensity. Thankamani (2000) screened black pepper varieties for water stress tolerance using photosynthetic parameters. She observed that varieties Poonjarmunda, Panniyur 5 and Kalluvally showed lower stomatal conductance while Panniyur 1, Kumbhakodi and Padappan recorded relatively higher stomatal conductance. When severely water stressed, the variety Kumbhakodi and Padappan showed higher transpiration rate.

2.8 Biochemical parameters

The transformation from vegetative to reproductive phase has been reported to change the status of biochemical constituents in plants. Analysis of plant extracts for various biochemical constituents therefore, help in better understanding of the metabolism, since the levels of these biochemical constituents in plant tissues at any given time is the outcome of their biosynthesis, accumulation and metabolism. Several researchers have emphasised that the plant part or age determines the levels and nature of endogenous constituents. Determination of various biochemical constituents in different parts of the shoot such as leaves, stem, fruit etc. is desirable in understanding biochemical status of the tree.

The level of nitrate reductase activity (NRA) in many crops has been positively correlated with their productivity. Raju and Rajagopal (1988) studied the nitrate reductase activity (NRA) in the flag leaves and berries of black pepper during growth and development. NR activity in the berry increased while that in the flag leaf declined with the time of development. The flag leaf irrespective of its age had higher NRA during the early stages of berry development and this decreased with the maturation of berries. Thomas (1990) reported that there was marked variation in NRA of Panniyur 1 in different months. The peak activity was noticed in February and a lower peak in August. The mean nitrate content of leaves was found to be high during the month of December and March while the least nitrate content was observed in September. Pattern of NRA indicated seasonal variation between varieties. There was also variation among the varieties with respect to NRA in runner shoot, plagiotrope and orthotrope. It was also observed that varieties with higher flag leaf NRA had a higher NRA in berries. In general, there was an increase in NRA with increase in light intensity. A significant positive correlation between NRA and yield also was obtained.

Chempakam *et al.* (1998) analysed piperine content in black pepper berries from 120 days after flowering (120 DAF) until maturity (240 DAF) at 30 days interval. The content of piperine was less during early stages, and reached a maximum at 210 DAF. Activity of Phenylalanine Ammonia Lyase (PAL), a major enzyme in the biosynthesis of piperine precursor, was high in berries compared to leaves in the early stages. Volatile oil in berries declined with maturity while oleoresin showed about 50-60 percent increase after 180 DAF.

2.8.1 Chlorophyll content

Chlorophyll content in leaves varies with day length, irradiance, quality of light, temperature and nutrient status of soil (Lewandowska and Jarvis, 1977).

In black pepper, a reduction in chlorophyll and carotenoid pigments were observed due to higher temperature (Vasantha *et a*l., 1989 and Vijayakumar and Mammen, 1988). Thankamani (2000) reported a total chlorophyll content of 1.21mg g^{-1} of which chlorophyll 'a' and chlorophyll 'b' were 0.70 mg g^{-1} and 0.45 mg g^{-1} respectively in the leaves of non stressed plants. Chlorophyll content decreased in all the varieties due to stress.

In ginger, Xizhen *et al.* (1998 b) reported that the chlorophyll content and photosynthetic rate of leaves increased with increased leaf expansion to reach a peak in 15 days old leaves but subsequently declined gradually.

In grapes, Hunter and Visser (1989) reported that chlorophyll 'a' content decreased as leaves were situated progressively deeper into the canopy. No consistent relationship between chlorophyll concentration, light intensity and photosynthetic activity could be found for the different leaf position. In 15 grape genotypes studied, Giridharan, (1993) observed that the chlorophyll content was 3 mg g^{-1} in almost all the genotypes in 30 day old leaves. Schubert *et al.* (1996) in grapes reported that leaf chlorophyll content per unit leaf area was highest in leaves of intermediate age (40-60 days). Leaf chlorophyll contents in grapes were highest in 20 to 30 day old leaves (Lovisolo *et al.*, 1997).

The chlorophyll content in the leaves of cashew varieties screened for drought tolerance had high total chlorophyll content of above 3 mg g^{-1} of leaf tissue (Latha, 1998).

A positive correlation between leaf chlorophyll content, photosynthesis and biomass production has been reported in *Butea monosperma*, and *Acacia catechu* (Agarwal and Prakash, 1980). Leaf chlorophyll content, net photosynthetic rate and biomass production was estimated at monthly interval in seven tropical deciduous tree crops. The chlorophyll content of leaves expressed in area or fresh weight basis was significantly high in all the seven tree species during summer than in winter. Chlorophyll concentration showed marked variation from month to month and these differed from one plant species to another. Clear positive correlation was found between chlorophyll content and net photosynthetic rate and / or biomass production in all the species studied (Naidu and Swamy, 1995).

2.8.2 Carbohydrates and starch

Flowering and fruit development drain out a large amount of carbohydrates from the tree, as this requires 40 to 50 times more food reserve compared to vegetative growth (Shivshankara and Mathai, 1997). Hence more reserve carbohydrates are required for good flowering, fruit set and yield of a tree. Involvement of carbohydrates in flowering and strong and positive correlation between carbohydrate concentration of trunk, roots and leaves has been reported in various fruit trees (Kandiah, 1979., Scholefield *et al.,* 1985., Oliviera and Priestly, 1988 and Whiley *et al.*, 1989).

In black pepper, Daggade (1999) reported varietal variation in the sugar content of leaves. Reducing sugar content of leaves was higher in the variety Kalluvally (3.048 mg g^{-1}) compared to Karimunda (2.15 mg g^{-1}). However, non reducing sugar content was higher in Panniyur 1 (1.944 mg g^{-1}) compared to Kalluvally (1.636 mg g^{-1}). Thankamani (2000) also reported variation in the total sugar content of leaves among black pepper genotypes and also with the stress levels induced. The variety Panniyur 1 recorded 28.8 mg 100 mg^{-1} of total sugars.

The reducing sugar content of grape leaves can be used as selection criteria for screening at early stages against anthracnose (Daulta and Chouhan, 1981). The disease intensity was positively correlated with the content of reducing sugar (Jindal and Santhanam, 1993).

In fruit trees, particularly apple and mango, there is a longstanding evidence to suggest an association between high carbohydrate and starch levels in plant and tendency to flower (Singh, 1978 and Mishra and Dhillon, 1978). Suryanarayana (1978) reported that glucose and fructose contents decreased in the shoots of regular bearing cultivars Banglora and Neelum as well as irregular bearing cultivars Mulgoa and Banganapalli, at the time of flower bud differentiation. But during inflorescence development and emergence, the content of these sugars rose sharply. Ravishankar and Rao (1982) observed that insoluble carbohydrate fraction declined during the period of flower bud differentiation along with non-reducing sugar fraction resulting in a marked increase in the level of reducing sugars. Patil *et al.* (1991) also observed decreased content of reducing and non-reducing sugars during flower bud differentiation whose levels were higher before the onset of flower bud differentiation.

2.8.3 Phenols

Some of the phenolic compounds are analogous to plant hormones. Some may function as growth inhibitors as they invoke enhanced enzymatic oxidation of IAA and auxins and are reported to influence the flowering process. There also exist synergism between phenols and IAA (Bernier, 1988).

Phenolic compounds are present in black pepper as secondary metabolites. These are aromatic compounds formed via Shikimic acid pathway or Malonic acid pathway. These nitrogen containing secondary products are biosynthesised primarily from amino acids (Shoukathali, 1997). Daggade (1999) reported that the total phenol content of leaves was higher in the genotype Kalluvally (3.802 mg g^{-1}) compared to Panniyur 1 (2.483 mg g^{-1}).

The phenol and reducing sugar content of grape leaves can be used as selections criteria for screening at early stages against anthracnose (Daulta and Chouhan, 1981). The disease intensity was positively correlated with the content of reducing sugar and negatively correlated with total phenol content in leaves (Jindal and Santhanam, 1993). Giridharan (1993) observed that the total phenol content varied from 2.90 mg g^{-1} to 5.03 mg g^{-1} among grape cultivars. Phenolic compounds contributed to an increase in stomatal resistance under water stress (Brigidina and Kushnirenko, 1993).

2.8.4 Amino acids and proteins

Depending upon leaf age and other nutritional parameters, amino acids are the major translocated photosynthetic products and hence, directed in large amounts to apical meristems (Bernier, 1988).

Free amino acids of ten black pepper cultivars were characterised and quantified by Vasantha *et al.* (1991). They reported profiles of ten amino acids in pepper leaf. Daggade (1999) reported that among the plant parts analysed, leaves had a higher content of amino acids and the cultivar Kalluvally had higher content (0.35 mg g^{-1}) of amino acid in the leaves compared to Panniyur 1 (0.30 mg g^{-1}). Thankamani (2000) also reported variation in amino acid content of leaves with the genotypes and the level of stress induced. The amino acid content of leaves in the variety Panniyur 1 was 2.3 mg 100 mg^{-1}. The amino acid content showed an increasing trend due to severe stress in the varieties Panniyur 1, Panniyur 5 and Poonjarmunda.

Sen *et al.* (1972) observed high concentration of amino acids during vegetative growth in mango in summer, which showed appreciable decline during autumn and winter, which coincided with the fruit bud differentiation period. Maiti and Sen, (1978) noted promotion of flowering with the amino acids L-Methionine and Ascorbic acid which are believed to stimulate endogenous production of ethylene. Suryanarayana and Rao (1976) found a decrease in the content of amino acid on or before the flower bud formation, which was attributed to their increased utilisation for protein synthesis, essential for metabolic processes leading to onset of flowering. Mishra and Dhillon (1978) also reported qualitative changes in the content of free amino acids. They noted that off year mango leaves had lower levels of amino acids. While explaining the reasons for lower amino acid content, when the phenol content was high, they have stated that amino acids provide the basic material for synthesis of various mono and polyphenols in the plant system. They could not find any relationship between protein and fruit bud differentiation. Rao *et al.* (1982) reported a marked qualitative and quantitative increase in amino acids during the process of flower bud differentiation, which declined after the emergence of flower panicles in Alphonso mango shoots. The level of total amino acids content of the differentiating mango buds decreased during November indicating their faster utilisation in the formation of soluble protein during this period. Patil *et al.* (1991) studied the changes in the total free amino acid and protein content during fruit bud differentiation. They noted that there was a significant increase in total free amino acids in buds.

The role of free amino acids in berry growth in grapes was examined by Pandey *et al.* (1974). They have observed that free amino acids increased continuously from anthesis to the ripening of berries. Shiraishi (1991) examined the concentration of free amino acids and other chemical constituents in 75 grape cultivars at maturity. The total amino acid content varied between 3391 µ m and 5083 µm. Giridharan (1993) observed that the totals free amino acids in the leaves varied from 190 $\mu g\ g^{-1}$ to 541 $\mu g\ g^{-1}$ in leaves. When three year old potted *Vitis vinefera* cv. Freisa plants were subjected to varying light intensities 65 days after bud break, leaf protein contents were highest in 20 to 30 day old leaves (Lovisolo *et al.*, 1997).

Naidu and Swamy (1995) analysed the relationship between leaf soluble protein content and net photosynthetic rate in seven tropical deciduous tree species. The leaf protein content and net photosynthetic rate in *Terminalia arjuna* exhibited a significant positive correlation between leaf protein content and net photosynthetic rate.

2.8.5 Electrophoresis

In recent years protein and isoenzyme analysis by polyacrylamide gel electrophoresis (PAGE) has been considered as a unique and powerful technique for ascertaining gene homology at molecular level because of its superior capability per component resolution. Further, PAGE provides an additional tool for species identification and delineation, and has been particularly helpful in deducing systematic relationship between groups where morphological and cytological data are or not corollary. More over, the high stability of the seed protein profile and its additive nature make this method more reliable. In view of this, innumerable taxonomists have successfully established the phylogenetic relationship employing protein electrophoretic studies in major crops. Cereal crops have been extensively investigated to such extent that electrophoresis is widely used to check the pedigree or varietal identity and seed purity of cereal grain in trade for the purpose of registration, plant variety and utility patents (Yupsanis *et al.*, 1992). An understanding of the correlation between some desirable traits and enzyme banding pattern may also provide valuable information for early evaluation of hybrid progenies.

Seed protein isoenzyme electrophoresis have been used in cereal crops such as rice (Yupsanis *et al.*, 1992), wheat (William *et al.*, 1993) and maize (Smith, 1998) for varietal or cultivar identification. In legume crops, there are several reports on characterisation of cultivars, varieties and species of peas, beans and cow pea using various seed protein electrophoretic methods (Cooke, 1988., Ogbiake *et al.*, 1993 and Odeigah and Osanyinpenju, 1996). Chen *et al.* (1990) investigated 27 species of *Gossypium* and found that seed protein banding patterns were similar within species but differed between genus. Datta *et al.* (1992) evaluated the electrophoretic seed protein profiles of control and mutant lines of *Sesamum indicum* L. by polyacrylamide gel electrophoresis. The results revealed dissimilar seed protein profiles of band types, band number and relative mobility values for control and mutant lines. Eight varieties of *Anethum graveolens*, an important medicinal plant, have been characterised by electrophoresis (Manju *et al.*, 1993). There was significant variation between varieties in seed protein content and protein profiles were also qualitatively different between varieties.

The seed protein profile of eight taxa of chilli obtained by disc gel electrophoresis was found to be a diagnostic character in the study of phylogenetic relationships (Panda *et al.*, 1986). Characterisation of Nigerian varieties of capsicum by SDS PAGE seed protein was reported (Odeigah *et al.*, 1999).

2.9 Carbon translocation and partitioning using tracer studies

Considerable use of isotopes has been made by plant physiologists in studies on the photosynthesis and carbon partitioning in several crop plants. Among the many isotopes, the one that has been used frequently is the radioactive carbon ^{14}C. Several studies have been conducted using ^{14}C on different horticultural crops.

In black pepper, Mathai *et al.* (1988) studied the translocation of photosynthates at 45 and 150 days after initiation of the first spike in variety Karimunda. Forty per cent of the activity was retained in the fed leaf and about sixty per cent was translocated to other organs in 24 hours after feeding, at 45 days after spike initiation. The developing spike in the axil of fed leaf received 9.79 per cent of the radioactivity. At 150 days stage, the fed leaf retained 3.96 per cent and the subtending spike received 37.63 per cent radioactivity after 24 hours.

Distribution of labelled assimilates within a young apple tree after supplying $^{14}CO_2$ to a leaf or shoot was traced by autoradiography (Jankiewicz *et al.*, 1967). It was observed that the transport of labelled assimilates from the young leaves of the leader was very meagre and was traceable only in parts of the stem and the leaves situated in the close vicinity of the treated leaves. The translocation and distribution of ^{14}C labelled assimilates within a single shoot and between two adjacent shoots were studied in one year old Golden Delicious apple trees (Manolov *et al.*, 1974). When $^{14}CO_2$ was introduced into an upper developed leaf, the translocation of labelled assimilate was basipetal and when introduced into a lower leaf, acropetal. When whole shoots were exposed to $^{14}CO_2$, the labelled compounds were not translocated to adjacent shoot but moved into the roots.

Distribution of ^{14}C assimilates from individual leaves to clusters in grape shoots were investigated by Motomura (1990). Export of ^{14}C from the leaves and the percentage of distribution into the clusters increased with the number of clusters in shoots. Each cluster obtained ^{14}C assimilates mostly from the leaves on its own side of the shoot. Each of the clusters obtained 69-98 percent of assimilates from the leaves on its own side of the shoot, regardless of the relative position of the clusters on the shoot. The movement of labelled photosynthesis and carbon partitioning with in grape canopy was investigated (Stewart et *al.*, 1996) in potted grape cv. Reisling. Bi-directional translocation of ^{14}C photo assimilates was demonstrated. Minimal translocation of ^{14}C assimilates from source leaves in non-fruit bearing shoots was directed towards the clusters located on the lower shoot. However, it is suggested that the non fruit bearing shoots were contributing to the carbohydrate reserves in the roots where an allocation of more than 50.0 per cent is exported.

Studies on partitioning of $^{14}CO_2$ phtotosynthates were conducted in tea (Sanderson and Sivipalan, 1966), cocoa (Sleigh *et al.*, 1984), cardamom (Vasanthakumar, 1986) and Mango (Schaffer *et al.*, 1997). In strawberry, Schaffer *et al.* (1985) and Nishizawa *et al.* (1998) observed that carbohydrates accumulated in the previous season in the roots are mainly utilised for the initial vegetative growth and flowering.

2.10 Correlation studies

Kanakamany (1982) observed the morphological characters of 45 varieties of black pepper grown in Kerala including Panniyur 1 and Karimunda. The variability in 29 quantitative and 17 qualitative characters were analysed and four quantitative and five qualitative characters were selected for the formation of a key to describe and identify pepper varieties.

Significant positive correlation between spike number, number of developed berries per spike and yield has been reported (Ibrahim *et al.*, 1985 a).

Heritability and genetic advance were assessed for various quantitative characters such as spike length, berry weight, number of berries per spike, number of spikes and spike yield (Ibrahim *et al.*, 1985 b). Spike yield and spike number have shown maximum genotypic and phenotypic variability but lowest values of heritability (0.30 and 0.28 respectively). Berry weight had shown highest value for heretability (0.81) but minimum genotypic and phenotypic variability. The character spike yield was found to produce highest advance in the expression (51.34%) in selection, whereas only marginal improvement need be expected for berry weight (32.73%). Most of the quantitative characters showed moderate heretability in open pollinated seedling progenies while in F1 hybrids many of the productive traits showed negative values for heritability.

Path analysis of some yield components in the crop involving 133 seedling progenies of 3-8 years age group was conducted at pepper research station, Panniyur (Ibrahim *et al.*, 1985 c). The study revealed that the number of spikes per vine, length of spike and number of developed berries per spike were the most important characters influencing net yield. The yield components such as spike length, spike number etc., was found to have a direct effect on yield followed by number of developed berries per spike. Spike length was negatively correlated with yield. Hence it showed that the yield was not dependent on spike length and depends more on the number of developed berries per spike. On the basis of the relative contribution of components on yield, the character spike number is to be given preferential consideration over others as an index in selection for high yielding types. However, when characters like the number of developed berries per spike that is likely to show intra-varietal variability are considered, the spike number should also be given importance.

Sujatha (1991) and Sujatha and Namboothiri (1995) reported that characters such as green berry yield per vine, no of spikes per vine, length of spike, number of developed berries per spike and thickness of node and internode of orthotrope registered a high positive correlation with yield. The interrelationships among the characters too were high and positive. These findings point to the possible advantages of selection based on these characters for higher productivity of pepper plants.

Correlation between morphological and berry characters were reported in many fruit crops. In grapes, phenotypic correlation and heritability of certain qualitative traits were estimated in the progenies of cross between *Vitis vinefera* and *Vitis rotundifolia.* High heritability was observed for cluster compactness, berry weight and skin texture (Firoozabady and Olmo, 1987). Sandhu and Chanana (1992) observed that the morphological characters such as cane length, number of nodes per cane, number of laterals per cane and internodal length showed positive correlation with yield in grapes. Edson *et al.* (1995 b) observed that leaf area per vine, leaf size, shoot length, number of nodes and internodal length were inversely related to crop load. Fruit number per cluster and cluster weight was inversely correlated with cluster number per vine.

The useful areas of morphological, physiological and biochemical parameters as secondary characters for indirect selection has been reported in different species by various workers (Majumdar and Sharma 1990., Nazeer *et al.*, 1993 and Giridharan and Jindal, 1995).

From the available literature it can be concluded that flushing, flowering, fruit growth and development are complex processes influenced by wide range of physiological and biochemical factors with in the plants and the prevailing climatic condition as suggested earlier by various workers. Hence defining the growth and development, and identification and quantification of physiological and biochemical characters that influence productivity in black pepper may serve some useful result.

Materials and methods

MATERIALS AND METHODS

The present investigations on "Physiological and biochemical aspects of flowering, berry set and development in black pepper (*Piper nigrum* L.)" were carried out at the Department of Plantation Crops and Spices, College of Horticulture, Vellanikkara and Pepper Research Station (PRS), Panniyur during the period from 1997 to 1999.

Black pepper variety Panniyur 1 (P1), a hybrid developed at PRS, Panniyur, and Karimunda (KM), a popular cultivar of Kerala were selected for the study. Twenty vines each from the two varieties were selected at random from two experimental blocks of PRS, Panniyur from concluded trials. The experimental site has a typical tropical humid climate with unimodal monsoon rains aggregating to about 350 mm year^{-1}. The rainfall data for 1997 and 1998 at PRS, Panniyur are given in appendix I. The soil of the experimental site is acid laterite of clay loam texture. The selection of the vines was based on their uniform age and yielding ability and freedom from pests and diseases. The vines were in the age group of 8 to 10 years, trailed on *Erythrina indica* standards and planted at a spacing of 3m x 3m. They were grown under open conditions and were rain fed. The height varied from 4.5 m to 6.0 m. The vines were managed under uniform cultural and manurial practices as per the recommended package of practices (KAU, 1996).

The experiment was laid out in Completely Randomised Design (CRD) with two varieties and 25 individual plant replications per variety. Of the 25 plants, ten plants were utilised for sampling for growth analysis and biochemical studies. The remaining 15 plants were utilised for recording the morphological characters and photosynthetic parameters.

Observations were made to assess the growth, development, yield characters and production during flushing and flowering, berry set, berry development, maturity and harvest. The morphological characters as well as photosynthetic and biochemical parameters were determined at different canopy levels.

3.1 History of experimental plants

The yield data of the observational plants for the period from 1993 to 1997 was collected from the records available at PRS, Panniyur and tabulated.

The growth character of the vine was measured during pre flowering stage in the month of May. The number of laterals and the number of leaves on the laterals selected from all the sides were counted for twenty laterals from each canopy. The average of this was used for arriving at the total number of leaves per canopy. From these, the total leaf area of the vine was worked out as follows:

The length and maximum width of 20 leaves collected from each canopy level from the observational plants were measured. The corresponding area of the leaf was measured using a portable leaf area meter (Licor- LI 3000A) (plate 1) and the factors were computed for Panniyur 1 and Karimunda.

The leaf area was estimated by multiplying the product of length and maximum breadth with a constant 0.7 (Rao and Sebastian, 1994).

Leaf area = LxBxC
Where L = length of leaf
B = maximum width and
C = constant.

The leaf area of the lateral m^{-3} of the vine was calculated by multiplying the number of leaves with average leaf area and the number of laterals m^{-3}. The total leaf area of the vine was computed by summing up the individual part wise leaf area. This was expressed in cm^2.

3.2 Chronological events in the growth and development of the lateral

The events that occur in the lateral from initiation to the completion of growth during the season were traced.

Observations were made to assess the growth and development attributes of the leaf, spike and stem of lateral, during the stages covering flushing and flowering (June-July), berry set (August), berry development (September-October) and berry maturity (November-December). Fifteen plants each of the variety Panniyur 1 and Karimunda were selected for recording observations on vegetative flushing and extension growth of laterals.

Fifteen shoots, which were distributed on all sides of the canopy and exposed to sunlight, were selected from a plant for the study. The flushes that emerged on each lateral were selected at random and tagged serially on the day of their release from the leaf sheath. Flushes emerged on the same day were tagged in each canopy level. For better visibility of the tagged shoot, such laterals were tied with a piece of coloured ribbon cloth. Subsequent flowering activity and extension growth were monitored in the tagged flushes. Each tagged lateral was observed at fortnightly interval for production of leaves and spikes. The extension growth of the lateral was monitored at weekly interval till the attainment of maximum shoot length, i.e. up to the stage when two consecutive observations recorded were same.

3.2.1 Flushing

Sprouting of buds was observed at the onset of monsoon. The date on which at least 10 per cent of the total laterals have initiated flushing was noted as the date of flushing. Flushing was denoted by the release of the bud at the shoot apex from stipule in a curled form. The date of initiation of flushing was recorded in each vine at three days interval starting from June and entered as the date of initiation of laterals.

3.2.2 Leaf growth

The leaf area development was measured in cm^2 at weekly interval commencing from the date of flushing.

The leaf area of both intact as well as excised leaves was measured. Area of the leaves on the tagged laterals was measured from the day of full opening to the attainment of maximum area at weekly interval. The length and maximum width of leaf on a lateral were measured from the first day of unfurling and continued till there was no further increase in leaf area for two consecutive observations.

The leaf area was arrived at by multiplying the constant (0.7) suggested by Rao and Sebastian (1994) with the product of the length and maximum width.

The leaf area was also determined through destructive sampling. Twenty leaves from each canopy level of a vine were selected at random and tagged on the day of opening. They were sampled at weekly interval till they attained the maximum leaf area. Thereafter they were sampled at 15 days interval till berry maturity. The petioles of the collected leaves were removed. The leaf blade was measured with a portable leaf area meter (Model LI- 3000A) and also cross checked with manual computing by measuring length and maximum breadth.

3.2.3 Leaf fresh weight and dry weight development

Observations on fresh and dry weights of leaf were recorded at weekly interval, starting from first day of opening of the leaves to complete leaf area development. After this, the observations were made at 15 days interval till berry maturity, up to December. For this purpose, 100 leaves initiated within a week were tagged randomly from 15 standards of each variety and they were periodically sampled for fresh and dry weight assessment.

The leaves immediately after stripping were weighed for fresh weight. They were then washed and dried in a hot air oven at 60^0 C till constant weight was obtained. The dry weight of the leaves was recorded during each period sampled.

3.2.4 Leaf production and number of leaves

The number of leaves on the laterals at each canopy level was counted at fortnightly interval from flushing to the completion of leaf production. The number of leaves per lateral at the time of berry maturity was taken as the maximum number of leaves.

Plastochron index was computed by noting the time interval between the production of two successive leaves on a lateral and expressed as number of days.

3.2.5 Flowering, berry set and development

Flowering takes place in pepper with the onset of monsoon during June-July and the spikes develop from the axils of newly formed leaves of the laterals.

3.2.5.1 Initiation of flowering

The time of spike emergence was recorded when the spikes were emerged fully from the stipules in individual vines. This was observed at three days interval from the first week of flushing. The date of initiation of spikes was recorded in the tagged laterals in each selected vine.

3.2.5.2 Growth of spike

From each canopy level, 10 spikes were randomly selected and their length measured at weekly interval, from the first day of emergence of the spike to the period of attainment of maximum length of spike at each canopy level. The spikes those emerged on the same day were tagged and used for this purpose.

3.2.5.3 Sexual composition of spike

Ten spikes from each canopy level of a vine were selected at random for determining the sexual composition. The number of hermaphrodite, pistillate and staminate flowers and the total number of flowers in a spike were recorded and the respective percentages worked out. The annual variation in the sexual composition of the spikes was also found out by recording the observations during 1997 and 1998.

3.2.5.4 Weight of spike

The spikes in the laterals were sampled at fortnightly interval after berry set and were weighed individually for fresh weight, till the spike weights were constant for two subsequent observations.

3.2.5.5 Berry set

The time when ten per cent of the tagged laterals set berries were considered as the date of initiation of berry set.

3.2.5.6 Berry growth and development

Ten spikes each from a canopy level are tagged for sampling berries at fortnightly interval from berry set to maturity. One hundred berries were stripped off and counted from spikes collected from each canopy level and their fresh weight and volume were recorded. The berries were dried in a hot air oven at 60^0 C and the dry weight found out. The periodic accumulation of dry matter in the berries was arrived at.

3.2.5.7 Berry maturity and harvest index

The attainment of maximum berry volume and fresh weight, after which there was no further increase, was taken as the criteria of berry maturity. The period after berry maturity until a constant dry weight of berries was obtained was taken as the harvest index. The duration from berry set to maturity and harvest was recorded.

3.2.6 Extension growth and duration of growth of laterals

The length of five laterals at each canopy level from each vine was measured at fortnightly interval from flushing to the attainment of maximum extension growth of laterals. Length of a lateral is referred to as the length of the stem of a lateral in cm produced in the current flush.

3.3 Morphological parameters

Growth and yield attributes were recorded from fifteen vines selected from each genotype, at berry maturity. The total height of the vines excluding the basal portion devoid of laterals was measured by using a graduated PVC pipe. The canopy of the vines was arbitrarily divided into three equal parts as lower, middle and upper.

3.3.1 Growth and yield characters of the laterals

The portion consisting of the current season growth from the tagged laterals were separated from the vines from each canopy level at berry maturity and the following observations were recorded:

The number of leaves on the laterals was counted and the average worked out. The leaf area was estimated by using a portable leaf area meter (LICOR model LI – 3000A). The total leaf area of the lateral at berry maturity was obtained by multiplying the total number of leaves of the lateral with the average leaf area of that canopy level in a plant. The stem length of the excised lateral was measured and recorded as the length of a lateral in cm.

The total number of nodes from the base to the apex of lateral shoots was counted and the mean value recorded. The number of internodes in a lateral also was recorded. The average internodal length in a lateral was arrived at.

$$\text{Internodal length} = \frac{\text{Total length of a lateral}}{\text{Number of internodes}}$$

3.3.2 Accumulation of biomass and partitioning in the lateral

The total fresh weight of laterals was obtained by weighing the current season growth as a whole including the stem, leaves and spikes at berry maturity. The laterals were then separated as the stem, spike and leaves and weighed individually.

Each part was dried separately in a hot air oven at 60 ^{0} C till constant weight was obtained. The samples were weighed and dry weight of individual parts as well as total dry weight was recorded. From this, the partitioning percentage of leaf, stem and spikes were arrived at. Thus the total fresh and dry matter accumulated and those distributed to vegetative and reproductive parts were assessed.

The leaf dry weight per lateral was obtained as the sum of dry weight of individual leaves in a particular lateral. From this, the average dry weight of a leaf in a lateral was calculated.

$$\text{Average leaf dry weight} = \frac{\text{Total leaf dry weight of a lateral}}{\text{Number of leaves on the lateral}}$$

The dry weight per unit length of a lateral was calculated by dividing the total stem dry weight (g) by the length of the lateral in cm.

3.3.3 Spike characters and yield of vine

Spike and berry characters such as average spike weight, spike length, number of developed, underdeveloped, pollu affected and total number of berries per spike, volume and weight of 100 berries and dry weight percentage were recorded. The number and weight of green spikes and green berry yield was recorded for each canopy level at the time of harvest.

Dry weight percentage was worked out by sun drying one kg of cleaned green berries from each canopy level of the vine. From these observations, dry pepper yield was arrived at.

3.4 Physiological parameters

3.4.1 Specific leaf area (SLA)

The specific leaf area (SLA) of lateral was obtained by dividing the area of individual leaves in a lateral by their respective leaf dry weights. The average of this individual specific leaf area was reported as SLA of that particular lateral and was expressed in $cm^2\ g^{-1}$

$$\text{SLA} = \frac{\text{Area of individual leaf (cm}^2)}{\text{Leaf dry weight (g)}}$$

3.4.2 Specific leaf weight (SLW)

Specific leaf weight (SLW) of lateral was assessed by dividing the average leaf dry weight by the corresponding average leaf area in a lateral and expressed in $mg\ cm^{-2}$ leaf area.

$$SLW = \frac{\text{Leaf dry weight (mg)}}{\text{Leaf area (cm}^2\text{)}}$$

3.4.3 Leaf weight ratio (LWR)

The leaf weight ratio was computed using the data on final leaf biomass and total dry matter of the laterals.

$$LWR = \frac{\text{leaf biomass (g)}}{\text{Total dry matter of laterals (g)}}$$

3.4.4 Specific gravity of berries

The specific gravity of the berries was recorded as the ratio of fresh weight to the volume.

3.4.5 Spike to leaf ratio (SLR)

This was obtained by dividing the total number of spikes to the total number of leaves produced during a season on the lateral.

3.5 Gas exchange parameters

The photosynthetic rate was measured during flushing and flowering, spike elongation, berry set, berry development, maturity and harvest stages. All the photosynthetic parameters were measured using a portable photosynthesis system (IRGA Model - LCA 4., Analytical Development Co., England) with Parkinson broad leaf chamber (PLC) (plate 3).

The new shoots developed after flushing was divided into productive (spike bearing) and nonproductive (without spikes) laterals. Five such productive and nonproductive laterals were selected at random from all directions in each canopy level .The number of observational plants were limited to 15. The leaves were tagged on the day of their opening.

3.5.1 Recording gas exchange parameters

The top youngest fully expanded leaf was clamped to PLC and was exposed to direct sunlight. The position of the leaf after inserting into the chamber

Plate1. Portable leaf area meter Model LI 3000A

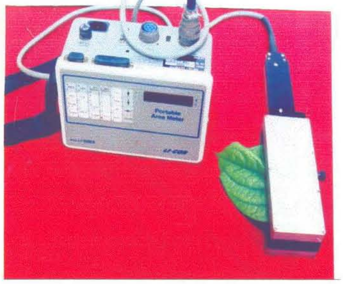


Plate 2. Leaf chamber fabricated for tracer studies

Plate 3. Portable photosynthetic system (IRGA- Model ADC 4) with Parkinson Leaf Chamber

was identical to its natural position. All the gas exchange traits were recorded under ambient conditions. Recording of data was done at saturated light intensities. Keeping in mind the possible diurnal variation of 'A' and g_s, all observations were made between 9.00 a.m. and 12.00 noon on a bright sunny day. The relative humidity (RH) in the leaf chamber was maintained at a steady state level around the existing ambient RH by manipulating the rate of flow of dry air through air supply unit of portable IRGA. Gas exchange parameters were recorded after 'A' and g_s stabilised to a steady state condition.

The following gas exchange parameters were studied :

a. Photosynthetic rate (A) in μmol $m^{-2}s^{-1}$
b. Stomatal conductance (g_s) in mol $m^{-2}s^{-1}$
c. Stomatal resistance (r_s) in m^2 s mol^{-1}
d. Transpiration rate (E) in mol $m^{-2}s^{-1}$
f. Leaf surface temperature in ^{0}C
g. P.A.R. on leaf surface (Q_{leaf}) in μmol $m^{-2}s^{-1}$
h. Sub- stomatal CO_2 concentration (Ci) in μmol mol^{-1}
i. Vapour pressure deficit (VPD) in mbar.

The measurements were recorded in the data logger attached to the instrument using built in software.

3.6 Biochemical studies

The leaves were tagged on the day of opening and samples were collected periodically at flushing and flowering, spike elongation, berry set, berry development, berry maturity and harvest stages. The new shoots developed after flushing was divided into productive (spike bearing) and nonproductive (without spikes) laterals. Five such productive and nonproductive laterals were selected at random from all directions in each canopy level.

3.6.1 Chlorophyll content

The chlorophyll content was estimated as per the method suggested by Sadasivam and Manickam (1996).

Leaf samples were collected from initiation to full leaf area development at weekly interval and estimation was carried out during the stages mentioned. The leaves were washed with distilled water and were dried using blotting paper. Uniform leaf discs of 0.5 g weight were taken from leaf blades avoiding mid rib and veins. This covered an approximate area of 0.5 cm^2 in mature leaves. The sample was immediately ground to a fine paste with a pinch of calcium carbonate in 5-10 ml pre-chilled 80 per cent acetone. Calcium carbonate was added to prevent pheophytin formation while grinding. The pulp was filtered and transferred to a 50 ml amber coloured volumetric flask. Repeated washings were done and the volume made up to 50ml.

The absorbance (A) of the extract at 645 nm and 663 nm was read in a spectrophotometer (Spectronic-20 genesis, Bausch & Lomb make) against the solvent acetone as blank. Using the absorption coefficients, the quantity of chlorophyll was calculated.

Chlorophyll content of the sample was estimated using the formula:

Mg. chlorophyll 'a' g^{-1} of tissue: $= 12.7\ (A_{663}) - 2.63\ (A_{645}) \times \frac{(1000 \times W)}{V}$

Mg. chlorophyll 'b' g^{-1} of tissue: $= 22.9\ (A_{645}) - 4.68\ (A_{663}) \times \frac{(1000 \times W)}{V}$

Mg. chlorophyll total g^{-1} of tissue $= 20.2\ (A_{645}) + 8.02\ (A_{663}) \times \frac{(1000 \times W)}{V}$

Where V = Volume of chlorophyll extracted in 80 per cent acetone

W = Fresh weight of tissue extracted

3.6.2 Total carbohydrates

Total carbohydrates were determined by Anthrone method (Sadasivam and Manickam, 1996).

Samples of 100 mg weight were ground in a mortar with pestle in 5 ml 2.5N hydrochloric acid. The pulp was transferred into a test tube and hydrolysed in a water bath for three hours and cooled to room temperature. It was then neutralised with sodium carbonate until the effervescence ceased and the volume was made up to 100 ml with distilled water. The supernatant was collected for estimation. Anthrone reagent was prepared by dissolving 200 mg Anthrone in 100 ml ice cold 95 per cent H_2SO4. Four ml of freshly prepared ice-cold Anthrone reagent was added to the solution and heated for eight minutes in a boiling water bath. It was then cooled rapidly and read for the intensity of colour at 630 nm in spectrophotometer (Spectronic 20, Genesis) using 4 ml Anthrone reagent as blank.

A standard graph was prepared using glucose for which 100 mg of D glucose was dissolved in 100 ml distilled water. A working standard was prepared by diluting 10 ml of the stock solution to 100 ml with distilled water along with a few drops of toluene. From that, 0.2, 0.4, 0.6, 0.8, and 1.0 ml were pippetted. Four ml Anthrone was added to it and kept for boiling for eight minutes in a water bath. It was then cooled rapidly and the intensity of colour was read at 630 nm. A standard graph was prepared using different concentrations and the absorbance recorded. From the graph, the corresponding concentrations of mg of glucose in the samples were obtained.

$$\text{The quantity of carbohydrates present in 100 mg sample} = \frac{\text{mg of glucose(from graph)}}{\text{Volume of test sample}}$$

3.6.3 Estimation of total phenol

The total phenol content was estimated using Folin- ciocalteau method suggested by Sadasivam and Manickam (1996).

Methanol extract of leaves was used for this estimation. A sample of 0.1 g was ground with 80 per cent methanol in a mortar with pestle. The homogenised material was centrifuged at 10,000 rpm for 20 minutes and the supernatant was evaporated to dryness. The residue was dissolved in 10 ml distilled water and 0.1 ml of the extract was incubated in the test tubes along with 3 ml distilled water and 0.5 ml Folin - ciocalteau reagent (commercially available) and 2.0 ml of 20 per cent Na_2CO_3 solution. The contents were mixed thoroughly, heated for one minute in a boiling water bath and then cooled in running tap water for the development of blue colour. The intensity of colour was measured at 650 nm after setting the reagent blank as zero. The total phenol content in the test solution was determined with reference to a standard curve prepared from different concentration of catechol and expressed as mg g^{-1} of fresh weight of sample.

3.6.4 Estimation of total free amino acids

The total free amino acid was determined in terms of leucine equivalents using the colorimetric method suggested by Sadasivam and Manikkam (1996).

Ninhydrin reagent was prepared afresh by dissolving 0.8 g of stannous chloride in 500 ml 0.2 M citrate buffer and adding this solution to 20 g ninhydrin dissolved in 500 ml methyl cellosolve.

One gram of the sample was extracted in 1 ml of 80 per cent isopropyl alcohol. The homogenised mass was centrifuged in a Kubota refrigerated centrifuge at 15000 rpm for 20 minutes. The supernatant was evaporated to dryness and the residue dissolved in 10 ml distilled water for further analysis.

One ml of ninhydrin was added to 1ml of the extract and heated for 20 minutes in a boiling water bath. Five ml of the diluent (50 ml isopropanol in 50 ml of distilled water) was added to it. After 15 minutes, the intensity of purple colour developed was measured at 570 nm against the reagent blank (2 ml 10% isopropanol + 2 ml ninhydrin + 10 ml diluent) in a spectrophotometer.

The concentration of amino acid in the sample was calculated from the standard curve prepared with different concentration of leucine.

3.6.5 Polyacrylamide gel electrophoresis of seed proteins

Five vines of each variety were used for the study. Spikes from the selected plants of varieties Panniyur 1 and Karimunda were collected separately in an ice bucket. After washing and rinsing with distilled water, the berries were stripped off and used for extracting samples to run the electrophorogram at different stages.

Two ml of buffer was used for extracting 2 g of sample using a mortar and pestle with insoluble PVP (0.1g), sucrose and 50 µl ß-mercapto- ethanol. The seed protein fraction was recovered by centrifugation at 4 ^{0} C in a Kubota refrigerated centrifuge. Supernatant was used immediately for electrophoresis.

Polyacrylamide gel electrophoresis was carried out using a mini gel (Hoefer scientific, USA) following the method described by Sadasivam and Manikkam (1996). The anionic system of 7.5 per cent running gel consisted of the following constituents:

a. Monomer

Acrylamide – 30.0 g
Bis acrylamide – 0.8 g
Total volume was made up to 100 ml and stored in a refrigerator.

b. Resolving gel buffer

Tris base – 18.5 g made up to 100 ml and
pH adjusted to 8.8 with 1 N HCl

c. Initiator

Ammonium persulphate (10%), prepared fresh
TEMED

The composition of 7.5 per cent gel (20 ml solution)

Monomer --- 4.98 ml
Resolving buffer --- 5.00 ml
Distilled water --- 4.94 ml
Ammonium persulphate --- 100 µl.
TEMED --- 10µl.

Electrophoresis was conducted in tris glycene buffer. The composition of the electrode buffer was as follows.

Tris – 6g
Glycine – 28.8 g
Volume – 1.0 litre
pH 8.3

The running was carried out at 5 ^{0} C with a constant current of 20 mA per gel plate. Running was carried out for 70 minutes.

Gel was then removed and stained with Coomassi brilliant blue G 250 (0.1%) in ethanol: phosphoric acid: water mixture (50 ml: 100 ml: 850 ml) and left as such overnight. It was destained for 30 minutes in a mixture consisting of acetic acid, methanol and water (1: 4: 5). Repeated washing and destaining was continued till clear banding was obtained. Electrophorogram was prepared and Rf values noted.

$$\text{Rf} = \frac{\text{Distance travelled by the band from top of gel}}{\text{Distance travelled by the dye from top of gel}}$$

3.7 Photosynthetic ^{14}C fixation

The rate of photosynthesis and the partitioning of photosynthates to various vegetative and reproductive organs in the lateral were studied by employing radio tracer technique using ^{14}C as the carbon source. The study was conducted in potted bush pepper plants of the varieties Panniyur 1 and Karimunda. The plants of each variety were fed with radioactive carbon at four stages viz., flushing, spike growth, berry set and berry development (Plate 4a-d). The flag leaf was selected at random from the laterals.

3.7.1 Leaf chamber fabrication

A leaf chamber was specially designed and fabricated for this purpose (Plate 2). The chamber was made using a metallic frame with mild steel, in rectangular shape. This consisted of a double walled chamber, of size 30 cm x 20 cm x 10 cm, as base. The top of the chamber consisted of glass of 4 mm thickness fitted on a frame for transmission of light which could be closed air tight. The glass lid was attached to the base using a rubber beading fitted into a groove cut around the periphery of the base of leaf chamber. A circulation system with cold water was provided with inlet and outlet through the double wall. A crescent shaped cut of 2.0 cm diameter was made on the top of the base on one side of the chamber to accommodate the leaf petiole. Another hole of 1.0 cm diameter was made on the other side and covered with an injection bottle rubber cap, as the hydrochloric acid inlet. The leaf intact on the potted bush pepper plant, could be enclosed in the

Stages of development of the laterals selected for tracer studies in bush pepper

Plate 4a. Flushing stage

Plate 4b. Spike growth stage

Plate 4c. Berry set stage

Plate 4d. Berry development stage

chamber through the crescent shaped groove provided in the front. Two chest latches held the base and the glass lid together.

A sleeve of sealed cell foam was placed around the petiole of leaf enabling the chamber lid to compress the sleeve and form a relatively tight seal around the petiole. The chamber was pre tested for leaks and was found to perform satisfactorily.

3.7.2 Feeding of radioactive carbon dioxide

Radioactive $Na_2\,^{14}CO_3$ (62.5 µci plant $^{-1}$) was kept in a petridish inside the leaf chamber. The specific activity of $Na_2\,^{14}CO_3$ used was 385.41 MBq m $^{-3}$.

One ml of $Na_2\,^{14}CO_3$ of 0.063 m ci activity was mixed with equal volume of non-radioactive Na_2CO_3 of the same concentration. The intact leaves were inserted into the leaf chamber. The leaf chamber was made airtight by closing the beaded lid and plugging the groove and petiole by sealed cell foam. Cold water was circulated to cool the air inside the chamber.

After setting the feeding system, hydrochloric acid was run down into the petridish containing radioactive $Na_2\,^{14}CO_3$ through a syringe attached to a drip bottle for which a provision was made with a rubber lid to the size of an injection bottle on one side of the chamber. I M hydrochloric acid (30 % v v^{-1}) was added sufficiently in excess in order to ensure that the reaction was complete. Sufficient quantity of radioactive $^{14}CO_2$ could be liberated from the $Na_2\,^{14}CO_3$ (385.41 MBq m $^{-3}$) with the addition of 1 M hydrochloric acid (Vosnizensky *et al.*, 1965). The reaction progressed as per the formula :

$$Na_2\,^{14}CO_3 + 2\,HCl\,O_4 \rightarrow \,^{14}CO_2 + 2\,NaCl + H_2O + 4\,O_2$$

The bush pepper plants were kept in open sun and the source leaf from each plant was enclosed in the specially fabricated chamber. The selected leaves were fed with the radioactive CO_2 and were allowed to assimilate the labelled CO_2 for 30 minutes. After specified duration, the unused mixture was purged through the exhaust tubes into 10 per cent KOH absorbent solution.

3.7.3 Estimation of radio activity

After feeding, the plants were brought into green house. The accumulation of photosynthates in different parts of the lateral at different intervals viz., 2 hours, 24 hours, 3 days, 5 days and 7 days after feeding were determined by destructive sampling of the laterals followed by radioassay. After the specified duration, the plants were separated into source leaf, subtending spike, lateral, root and other remaining plant parts. Each plant part was chopped and dried.

Dried samples were ground separately and 0.1g of each sample was weighed out and wrapped in a butter paper. The samples were combustioned at 700 ^{0} C in a biological oxidiser (Model DX 500, RJ Harvey Instrument Corporation, USA) and the released $^{14}CO_2$ were trapped in a vial containing scintillation cocktail as follows :

Ethanol amine (Scintillation grade)	– 300 ml
Methanol	– 300 ml
Toluene	– 1,000 ml
P P O	– 4.5 g
PO POP	– 250 mg

Radioactivity was measured in a scintillation counter (Model LKB 1409, Wallac, USA). The activities retained in the fed leaf and in different organs of the lateral were estimated. The import into the leaf and other parts was expressed as percentage of total radioactivity found in the whole plant.

3.8 Statistical analysis

The parameters analysed in the present study were grouped into morphological characters of vines and laterals and physiological and biochemical parameters.

Variation between genotypes viz., Panniyur 1 and Karimunda and canopy levels were analysed using 4 factor CRD in the M stat C package and tested for significance by using ANOVA (Panse and Sukhatme, 1989).

Correlation among all the combination of characters was computed using the Microsoft Excel software (98 version).

Various morphological, biochemical, photosynthetic and yield attributes of laterals was correlated with yield. Their interrelationships also were worked out.

The estimated values were compared with table values (Gomez and Gomez, 1984) at five and one percent probabilities. Characters, which showed significant correlation with yield, were identified.

Results

RESULTS

The results of the study on "Physiological and biochemical aspects of flowering, berry set and development in black pepper (*Piper nigrum* L.)", undertaken at the Department of Plantation Crops and Spices, College of Horticulture, Vellanikkara and Pepper Research Station, Panniyur are presented below:

4.1 History of experimental plants

The yield data of the experimental plants five years preceding the experiment are given in table 1a and fig. 1a. The average green berry yield per plant recorded were 1395 g and 1826g respectively, for Karimunda and Panniyur 1. The green berry yield differed significantly between varieties and over the years. The replications were not significant, indicating that the plants selected were uniform in their yielding ability.

The growth characters of the experimental plants such as height, number of main laterals per plant, girth of main laterals, number of leaves per plant, average leaf area and total leaf area per plant were recorded before the commencement of the experiment and are presented in table 1b.

The height of the plants varied between 5.04 m in Karimunda and 4.85 m in Panniyur 1. However, the height did not vary significantly either between varieties or replications.

The number of main laterals per plant was significantly higher in Karimunda. The number of leaves per plant and the total leaf area per plant also were significantly higher in Karimunda. However, the average individual leaf area was higher in Panniyur 1.

The varietal and canopy level differences in the number of leaves retained on the lateral and the length of laterals in terms of previous season's growth were also recorded before the commencement of the experiment and presented in table 1c and fig. 1b-c.

Table 1a. Pre-experiment yield data of the selected plants in black pepper varieties

Year	Green berry yield(g/vine)	
	Karimunda	Panniyur 1
1993	633	825
1994	840	1589
1995	1575	1203
1996	1803	3017
1997	2125	2495
CD	NS	
Average	**1395**	**1826**
CD	* 360.38	

Table 1b. Growth parameters of the plants before commencement of the experiment during May 1997

Parameter	Karimunda	Panniyur 1	CD
Height (m)	5.04	4.85	NS
Number of main laterals	106.88	89.03	** 15.59
Girth of main lateral (cm)	47.88	44.038	NS
Number of leaves	702.04	270.82	** 158.06
Average leaf area (cm^2)	46.66	87.42	** 8.49
Total leaf area (cm^2)	32910.70	23415.31	** 7618.27

Table 1c. Growth characters of the lateral before the commencement of the experiment

Canopy	Previous season length		Number of leaves	
	Karimunda	Panniyur1	Karimunda	Panniyur 1
Lower	12.2	4.83	1.77	0.98
middle	9.72	6.36	2.23	1.24
upper	8.42	6.59	2.37	1.37
CD	* 2.87		NS	
Average	**10.12**	**5.93**	**2.12**	**1.20**
CD	** 1.66		** 0.334	

History of the selected experimental plants in black pepper varieties

Fig. 1a Pre-experiment yield data

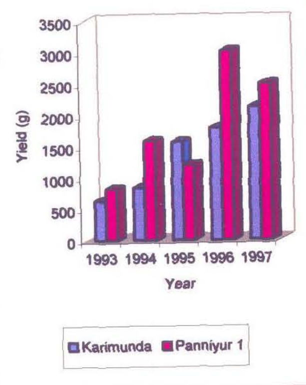


Fig. 1b Length of previous season lateral in different canopy levels

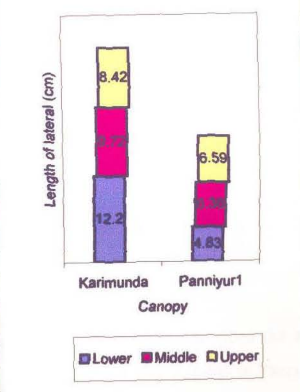
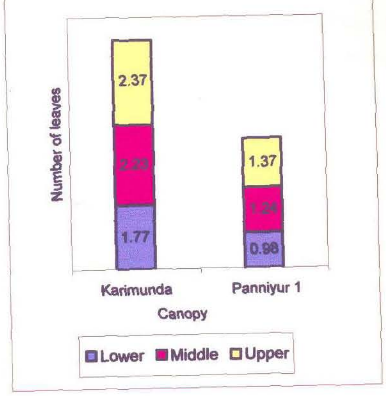


Fig. 1c Number of leaves in the lateral before the commencement of the experiment



The number of leaves retained on the laterals prior to the experiment, was significantly higher (2.12) in Karimunda than Panniyur 1 (1.20). The upper canopy retained more leaves compared to lower canopy in both the varieties.

The average length of past season's growth on the laterals was significantly higher in Karimunda compared to Panniyur 1. However in Karimunda, the growth of laterals was low in upper canopy levels producing shorter laterals.

4.2 Chronological events in the growth and development of laterals

Multiplicity of events took place during the course of development of the lateral during a season. This was broadly classified into flushing, leaf growth and development, flowering, spike growth and development and extension growth of laterals.

4.2.1 Leaf growth and development

4.2.1.1 Flushing

Flushing was indicated by the emergence of new leaves from the sheath situated at the shoot tip (plate 5a- b). The first flushing was noticed in Panniyur 1 on 11th June 1997. Among the varieties, Karimunda was six days late to initiate flushing in the tagged laterals (table 2) and the period of flushing also got extended further for six days compared to Panniyur 1. However, in both the varieties, flushing was initiated in the month of June itself, in all the plants.

During 1998 season, flushing was initiated on 3rd June itself. The pattern of flushing was similar to 1997 season with Panniyur 1 showing initiation early and delayed by six days in Karimunda. Flushing was initiated within a period of 18 days in all the laterals tagged. In general, the intense period of flushing was limited to mid July in Panniyur 1. However, moderate flushing continued further in Karimunda during the month of August and sparse flushing during September.

Plate 5a. Flushing in a lateral of Panniyur 1

Plate 5b. Flushing in a lateral of Karimunda

Plate 6a. Leaf area development in Karimunda

Plate 6b. Leaf area development in Panniyur 1

Plate 7a. Flushing and intiation of flowering in Karimunda

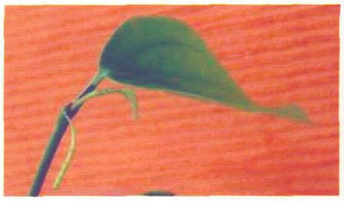


Plate 7b. Flushing and initiation of flowering in Panniyur 1

Table 2. Flushing of selected laterals in black pepper

Number of plants flushed					
1997			1998		
Date	KM	P1	Date	KM	P1
11-Jun	0	2	03-Jun	0	3
14-Jun	0	2	06-Jun	0	5
17-Jun	2	3	09-Jun	2	4
20-Jun	4	5	12-Jun	5	2
23-Jun	5	3	15-Jun	3	1
26-Jun	2	0	18-Jun	2	0
29-Jun	2	0	21-Jun	3	0
Total	**15**	**15**	—	**15**	**15**

Table: 3
Leaf area development in black pepper

Days after flushing	Leaf area (cm^2)		Increase in leaf area (cm^2)		Percentage increase	
	KM	P1	KM	P1	KM	P1
7	6.12	15.94	6.12	15.94	15.30	16.08
14	18.54	47.37	12.42	31.42	31.07	31.70
21	32.46	84.66	13.92	37.30	34.80	37.62
27	38.47	91.96	6.01	7.30	15.38	7.36
35	39.98	99.14	1.51	7.17	3.78	7.23
42	39.03	98.44	-0.95	-0.70	0.00	0.00
CD	** 6.73		—		—	

Leaf growth and development in black pepper

Fig. 2a Leaf area development at weekly intervals

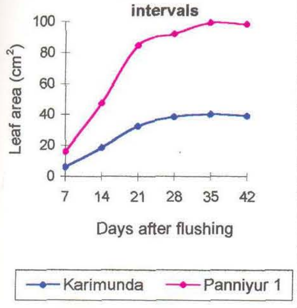


Fig. 2b Rate of increase in leaf area at weekly intervals

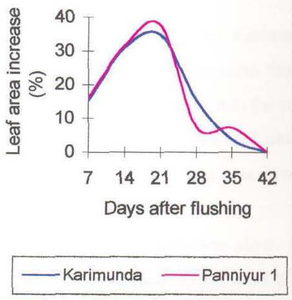


Fig. 3a Fresh weight development in leaves

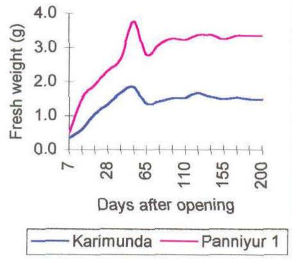


Fig. 3b Increase in fresh weight during leaf development

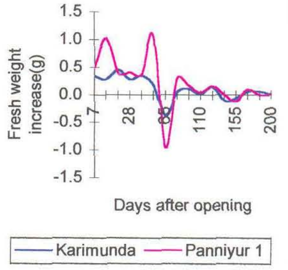


Fig. 4a Leaf dry weight development in black pepper

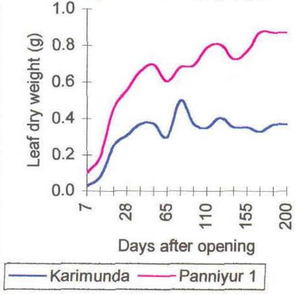
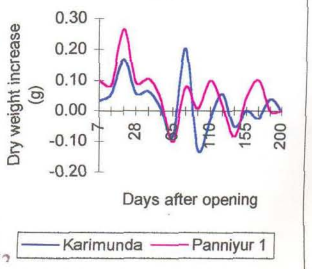


Fig. 4b Increase in dry weight during leaf development in black pepper



4.2.1.2 Leaf area development

The course of development of leaves after initiation to attainment of maximum leaf area was traced at weekly interval and the results are presented in table 3, fig. 2a-b and plate 6a-b.

The leaf area development showed similar pattern in Karimunda and Panniyur 1 wherein both the varieties took 35 days to complete the growth. Panniyur1 acquired larger leaf area compared to Karimunda within the same span of time indicating faster leaf growth rate. Even though the total leaf area differed significantly between the stages in the varieties, the rate of leaf area development was more or less same for both.

During the first week after initiation, leaf growth was slow, thereafter exponential during the second and third week covering 90 per cent of the total growth, and finally the growth rate declined.

The leaf area was measured using the portable leaf area meter. The leaf area constants for Karimunda and Panniyur 1 were worked out by dividing the leaf area by the product of length and maximum breadth. The constants were 0.68 for Karimunda and 0.71 for Panniyur 1.

4.2.1.3 Fresh and dry weight development in leaves

Fresh and dry weights of leaf increased continuously till the 50th day in both Karimunda and Panniyur 1 (table 4 and fig. 3a-b). Even though the period of leaf area development was 35 days, the weight development continued up to 50th day after emergence. Thereafter the fresh weight and dry weight of leaves showed a fluctuating trend. Fresh weight recorded was lower between 50-65 days and 125-155 days in Karimunda and 50-65, 95–110 and 140-155 days in Panniyur 1 compared to the previous stages. The fresh and dry weight of leaf differed significantly between varieties and stages. Leaf fresh weight was always higher in Panniyur 1 than Karimunda at all the stages observed. The maximum increase in fresh weight was between 14-21 days in Karimunda and 7-14 days in Panniyur 1. The fresh weight and dry weight of leaves were on par between the stages

Table 4. Fresh weight and dry weight development of leaves in black pepper

Days after initiation	Fresh weight (g)		Increase in fresh weight (g)		Dry weight (g)		Increase in dry weight (g)	
	KM	P1	KM	P1	KM	P1	KM	P1
7	0.34	0.49	0.34	0.49	0.03	0.10	0.03	0.10
14	0.60	1.52	0.28	1.02	0.08	0.19	0.06	0.09
21	1.05	1.91	0.45	0.39	0.25	0.46	0.17	0.27
28	1.32	2.31	0.27	0.41	0.31	0.55	0.06	0.09
35	1.67	2.68	0.34	0.37	0.37	0.66	0.06	0.11
50	1.85	3.76	0.18	1.08	0.38	0.70	0.01	0.04
65	1.37	2.80	-0.38	-0.96	0.30	0.60	-0.08	-0.10
80	1.41	3.09	0.04	0.30	0.50	0.68	0.20	0.08
95	1.52	3.26	0.11	0.17	0.37	0.69	-0.13	0.01
110	1.53	3.22	0.01	0.04	0.35	0.79	-0.02	0.10
125	1.67	3.38	0.14	0.16	0.41	0.81	0.06	0.02
140	1.56	3.38	-0.11	0.00	0.35	0.72	-0.05	-0.08
155	1.49	3.25	-0.07	-0.12	0.35	0.77	0.00	0.05
170	1.54	3.35	0.05	0.10	0.33	0.87	-0.02	0.10
185	1.48	3.35	0.05	0.00	0.37	0.87	0.04	0.00
200	1.48	3.35	0.00	0.00	0.37	0.87	0.00	0.00
CD	** 0.233		—		** 0.143		—	

observed after 80th day in both the varieties. There was no change in fresh weight of leaves after 185 days of leaf initiation in both Panniyur 1 and Karimunda.

The development of leaf dry weight showed a slightly different trend compared to that of fresh weight development (fig. 4a-b). The average dry matter production in leaves was highest during 80th day (0.50 g) in Karimunda and at 170th day (0.87 g) in Panniyur 1. The period of maximum increase in dry weight was between 14-21 days in both the varieties. The period between 50-65, 125-155 and 170-185 days in Karimunda and 50-65, 95-110 and 140-155 days in Panniyur1 showed lower dry weight than the previous stage.

4.2.1.4 Leaf production

The leaf production in the laterals during the season was traced and presented in table 5.

The average number of leaves produced in the laterals was significantly higher in Karimunda (3.67) than Panniyur 1 (2.23). However, the interaction between variety and canopy level was not significant. An increasing trend in leaf production was evident towards upper canopy levels. The leaf production with respect to canopy levels was more pronounced in Panniyur 1, which showed marked increase in leaf production at mid and upper canopy levels.

4.2.1.5 Plastochron index

On an average, the time interval required between the production of successive leaves in the varieties was 23.83 days (table 6). The leaf production per lateral was up to five in Karimunda, while this was a maximum of three in Panniyur 1. In general, the number of laterals that initiated flushing and produced leaves among the total laterals tagged was higher in Karimunda compared to Panniyur 1.

The time interval between the production of successive leaves increased from first leaf to subsequent leaves in both varieties. However, the number of days required for successive leaf production did not differ significantly between the varieties and canopy levels.

Table 5. Leaf production in the laterals

Canopy	Karimunda	Panniyur 1
Lower	3.50	1.85
Middle	3.55	2.30
Upper	3.95	2.55
CD	NS	
Average	**3.67**	**2.23**
CD	** 0.255	

Table 6. Plastochron index in black pepper

Canopy	Karimunda					Panniyur 1				
	Number of days					Number of days				
	leaf 2	**leaf 3**	**leaf 4**	**leaf 5**	**Average**	**leaf 2**	**leaf 3**	**leaf 4**	**leaf 5**	**Average**
Lower	18.05	22.36	24.20	27.50	**23.03**	21.60	22.50	0.00	0.00	**22.75**
Middle	17.30	26.94	27.27	26.00	**24.38**	21.75	27.16	0.00	0.00	**24.40**
Upper	16.80	25.25	26.90	27.25	**24.05**	22.75	27.50	0.00	0.00	**24.36**
Average	**17.38**	**24.85**	**26.12**	**26.92**	**23.82**	**22.03**	**25.72**	**0.00**	**0.00**	**23.84**
CD	** 1.61				NS	** 2.14				NS

4.2.2 Flowering, spike growth and development

4.2.2.1 Flowering

Flowering was initiated immediately after flushing in both Karimunda and Panniyur 1 (table 7). Flowering was indicated by emergence of the spike covered in a sheath, which fell off later. The interval between the emergence of leaf and the subtending spike was up to six days in Karimunda and nine days in Panniyur 1. However, there were instances of the spikes emerging first or simultaneously with the leaves, in a few replications (plate 7a-b).

Further production of spikes in a lateral occurred after the emergence of subsequent leaves in both the varieties and in such cases, spikes emerged strictly after leaf emergence, which resulted in sympodial nature of growth of the lateral.

4.2.2.2 Spike growth

The spikes after emergence from the sheath elongated rapidly and became pendent. The growth of spike was observed and presented in table 8, fig. 5a-b and plate 8a-b.

Spike growth was completed within 35 days in Karimunda and 42 days in in Panniyur 1. However, more than 90 per cent elongation took place within 28 days after initiation in both the varieties. The length of spike was 5.83 cm and 10.57 cm respectively for Karimunda and Panniyur 1. The rate of spike growth was similar for both the varieties in the first and second week after initiation. Karimunda and Panniyur 1 recorded 12.0 per cent and 11.8 per cent growth respectively during the first week and 27.46 per cent and 27.62 per cent respectively during the second week. The maximum growth rate of spike was between 14th and 21st day after initiation in both the varieties. During this period, 46.34 per cent and 33.72 per cent of the total spike length was achieved in Karimunda and Panniyur 1, respectively. The spike length differed significantly between varieties and stages up to 4th week. Growth rate was slow in both the varieties after this stage. In general, the growth of spike was exponential till 21st day and thereafter slow and then reached the minimum on 42nd day. Panniyur 1

Table 7. Initiation of flowering in black pepper

Date	Number of vines	
	KM	P1
11/06/97	0	1
14/06/97	0	2
17/06/97	2	4
20/06/97	2	3
23/06/97	3	1
26/06/97	2	2
29/06/97	5	1
02/07/97	1	1
Total	**15**	**15**

Table 8. Spike growth in black pepper

Number of days	Length of spike (cm)		Increase in length (cm)		% increase in length	
	KM	P1	KM	P1	KM	P1
7	0.71	1.25	0.71	1.25	12.00	11.80
14	2.31	4.17	1.60	2.92	27.46	27.62
21	5.01	7.74	2.70	3.57	46.34	33.72
28	5.70	9.75	0.69	2.01	11.82	19.02
35	5.82	10.35	0.12	0.60	2.10	5.64
42	5.83	10.57	0.01	0.23	0.17	2.13
CD	** 0.48		—		—	

Table 9. Sexual composition of spikes in black pepper

Sex	1997					1998				
	Number of flowers			Percentage		Number of flowers			Percentage	
	KM	P1	CD	KM	P1	KM	P1	CD	KM	P1
Bisexual	51.85	78.62	** 7.61	98.90	97.30	40.80	74.66	** 0.182	98.59	98.01
Female	0.55	2.18	** 0.95	1.10	2.70	0.58	1.51	NS	1.41	1.98
Male	0.00	0.00	NS	0.00	0.00	0.00	0.00	NS	0.00	0.00
Total	52.48	80.57	** 7.79	100.00	100.00	41.38	76.17	** 8.79	100.00	100.00

Spike growth and development in black pepper

Fig. 5a Spike growth at weekly intervals

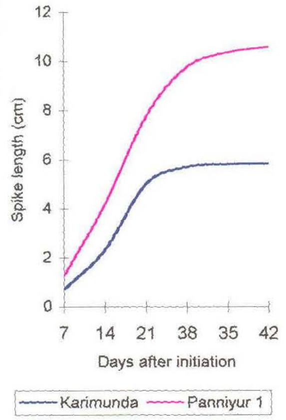


Fig. 5b Rate of increase in spike length at weekly intervals

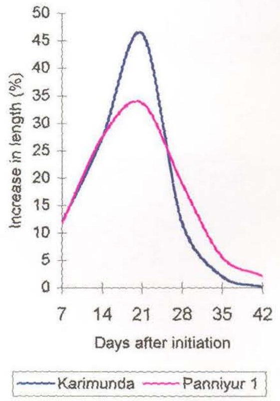


Fig. 6a Spike development in black pepper

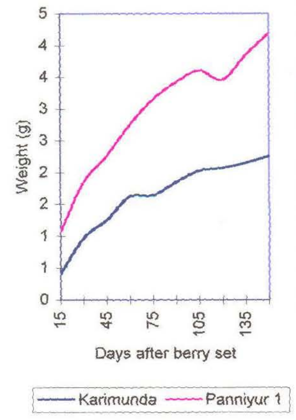


Fig. 6b Rate of fresh weight development in spikes

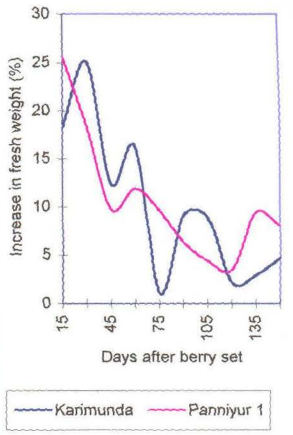


Plate 8a. Spike growth in Karimunda

Plate 8b. Spike growth in Panniyur 1

Plate 9a. Spike development in Karimunda

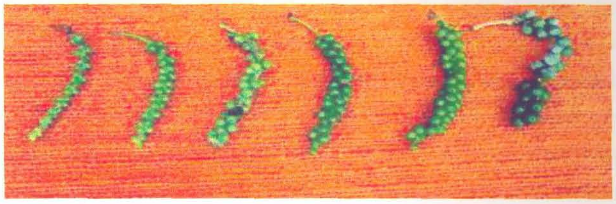
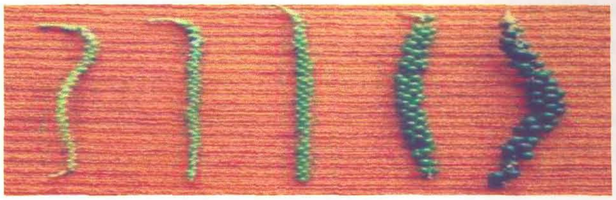


Plate 9b. Spike development in Panniyur 1



recorded higher rate of increase in spike length than Karimunda during all the stages observed.

4.2.2.3 Sexual composition of spikes

The sexual composition of spike was observed and presented in table 9. During 1997 season, 98.9 per cent and 97.3 per cent of the total flowers were bisexual and the female flowers were only 1.10 and 2.70 per cent in Karimunda and Panniyur 1 respectively. However, male flowers could not be observed in the spikes of both the varieties. The spikes of Panniyur 1 had more number of bisexual flowers on account of the longer spikes.

During 1998-99 also, there was no significant variation in the percentage of bisexual and male flowers between the varieties. This indicated that there is no seasonal effect in sexual composition of spikes.

4.2.2.4 Development of spikes

The increase in fresh weight of spikes was recorded at 15 days interval starting from berry set (1st of August) till berry maturity (table 10, fig. 6a-b and plate 9a-b). There was no significant variation in fresh weight of spikes after 165 days of berry set in Karimunda and 180 days in Panniyur 1. The fresh weight development in the spikes registered a similar pattern in both Karimunda and Panniyur 1. The maximum increase in the fresh weight of spikes was recorded during the first month after berry set in both the varieties. Karimunda and Panniyur 1 recorded 42.23 per cent and 40.56 per cent of the total fresh weight, respectively during this period. Thereafter, the rate of development gradually declined towards the month of December. Almost 80 per cent of total fresh weight was achieved within three months after berry set. This may be because the fresh weight accumulated by the spike also includes the stalk, which might have completed its growth in length within this period. After this, the rate of accumulation of fresh weight decreased except during 120th to 150th day in Panniyur 1, where the increase was more than the previous month.

Table 10. Fresh weight development in spikes after berry set

Days after berry set	Spike weight (g)		Increase in spike weight (g)		% increase	
	KM	P1	KM	P1	KM	P1
15	0.41	1.08	0.41	1.08	17.67	23.68
30	0.98	1.84	0.57	0.77	24.56	16.88
45	1.26	2.25	0.28	0.41	12.08	8.99
60	1.62	2.75	0.37	0.50	15.94	10.96
75	1.64	3.16	0.02	0.40	0.90	8.71
90	1.85	3.42	0.21	0.26	9.05	5.70
105	2.03	3.61	0.18	0.19	7.75	4.17
120	2.07	3.46	0.05	0.15	2.15	3.29
135	2.15	3.86	0.08	0.40	3.44	8.77
150	2.26	4.19	0.11	0.34	4.74	7.44
165	2.32	4.40	0.06	0.21	2.59	4.60
180	2.32	4.56	0.00	0.16	0.00	3.5
195	2.32	4.56	0.00	0.00	0.00	0.00
CD	** 0.354		—		———	

Table 11. Spike production in black pepper during 1997- 98 season

Canopy	Number of spikes	
	KM	P1
Lower	422.95	138.00
Middle	713.11	192.00
Upper	779.00	334.00
Average	**638.35**	**222.18**
CD	** 54.75	
Total	1915.06	664.00
CD	** 139.07	

4.2.2.5 Spike production

The total number of spikes at different canopy level and per plant were recorded and furnished in table 11. The number of spikes differed significantly between varieties and also between canopy levels. Spike production was more for Karimunda (638.35 nos.) compared to Panniyur 1(222.18 nos.). Spikes production showed an increasing trend from lower to upper canopy. Karimunda was significantly superior to Panniyur 1 in production of spikes at all canopy levels. However, the canopy level difference in production of spike was more pronounced in the variety Panniyur 1, as the upper canopy recorded more than twice the number of spikes compared to the lower canopy.

4.2.3 Berry set and development

4.2.3.1 Berry set

After pollination, the berry starts developing into globular structures. The berry set in the tagged inflorescence was observed for the period from third week of July to first week of August. The data gathered from the experiment indicated that the period from flowering to completion of fruit set in a spike was approximately six weeks in both Karimunda and Panniyur 1.

4.2.3.2 Berry growth and development

The growth and development of berries in terms of 100 berry fresh weight, dry weight and volume, from berry set to maturity was recorded and presented in table 12 and fig. 7a-b. The results indicated that hundred berry weight differed significantly between varieties and stages observed. The trend in fresh weight development was similar in both Karimunda and Panniyur 1. The fresh weight of berries increased up to 165 days in Karimunda and 180 days in Panniyur 1. The maximum rate of fresh weight development was during the period between 45-75 days in both Karimunda and Panniyur 1. An increase of 35.41 per cent and 40.77 per cent compared to the total fresh weight of berries was noticed in Karimunda and Panniyur 1 respectively, during this period. About 75.0 per cent of the total fresh weight was achieved in 90 days after fruit set in both the varieties. The rate

Table 12. Growth and development of berries after berry set

Days after berryset	100 berry fresh wt. (g)		Increase in weight (g)		% increase		100 berry volume (cc)		Increase in volume (cc)		% increase		100 berry dry wt. (g)		Increase in dry wt. (g)		% increase	
	KM	P1	KM	P1	KM	P1	KM	P1	KM	P1	KM	P1	KM	P1	KM	P1	KM	P1
15	0.97	1.24	0.97	1.24	10.18	8.68	1.10	1.19	0.76	21.04	11.16	8.37	0.20	0.21	0.20	0.21	7.18	4.75
30	2.33	2.53	1.36	1.30	14.37	9.10	2.07	2.69	0.98	1.50	9.88	10.62	0.27	0.36	0.07	0.16	2.67	3.68
45	3.47	3.70	1.14	1.17	12.03	8.20	3.19	4.56	1.12	1.88	11.32	13.25	0.40	0.47	0.13	0.11	4.74	2.52
60	5.16	7.76	1.69	4.06	17.81	28.53	4.96	7.53	1.78	2.96	18.03	20.93	0.77	1.09	0.37	0.61	13.54	14.23
75	6.84	9.51	1.67	1.74	17.60	12.24	7.03	9.78	2.06	2.26	20.90	15.96	1.14	1.47	0.37	0.38	13.57	8.87
90	7.55	10.49	0.71	0.98	7.48	6.88	7.58	10.24	0.55	0.46	5.58	3.25	1.38	1.67	0.23	0.20	8.54	4.70
105	8.13	10.90	0.58	0.41	6.12	2.90	8.16	10.72	0.59	0.53	5.97	3.73	1.59	1.98	0.22	0.30	8.06	7.02
120	8.75	11.24	0.62	0.34	6.53	2.40	8.68	11.21	0.51	0.44	5.20	3.11	1.91	2.23	0.31	0.26	11.24	5.91
135	8.80	11.84	0.06	0.60	0.59	4.20	8.83	11.82	0.15	0.60	1.55	4.25	2.26	2.40	0.35	0.11	12.73	2.50
150	9.07	13.11	0.27	1.27	2.80	8.89	9.24	13.04	0.41	1.22	4.19	8.65	2.34	2.99	0.08	0.59	2.96	13.65
165	9.49	13.96	0.42	0.85	4.42	5.94	9.63	13.88	0.38	0.84	3.90	5.90	2.62	3.75	0.28	0.76	10.36	17.66
180	9.49	14.24	0.00	0.28	0.10	1.90	9.84	14.15	0.22	0.28	2.20	1.94	2.74	4.31	0.12	0.56	4.38	13.07
195	9.49	14.24	0.00	0.00	0.00	0.00	9.84	14.15	0.00	0.00	0.00	0.00	2.74	4.50	0.00	0.19	0.00	4.20
CD	** 0.247		—		—		** 0.437		—		—		** 0.106		—		—	

Growth and development of berries in black pepper

Fig. 7a *Fresh weight development in berries*

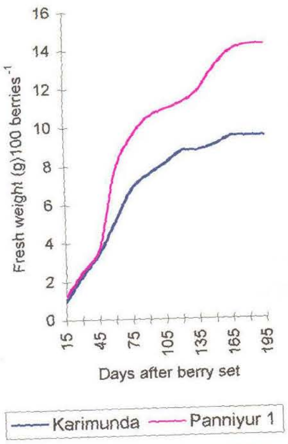


Fig. 7b *Rate of development of fresh weight in berries*

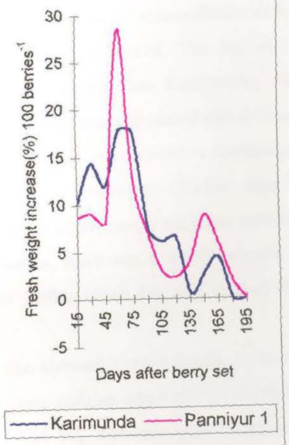


Fig. 8a Dry weight development in berries

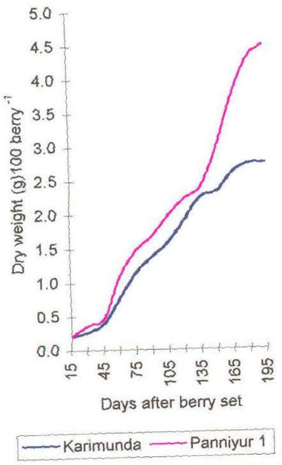
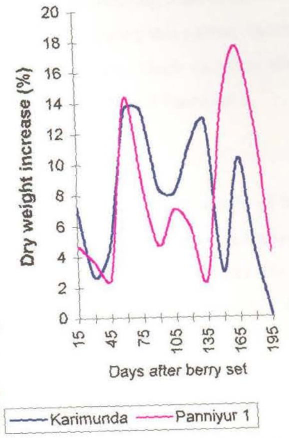


Fig. 8b Rate of dry weight development in beriies



of fresh weight development was comparatively slower after 90 days and was negligible after 150 days in Karimunda. However, in Panniyur 1, the increase was reasonable in the latter months also. So the development of the berries took longer time in the case of Panniyur 1.

The trend in dry weight development was slightly different from that of fresh weight and volume of berries (fig. 8a-b). The rates of accumulation of dry weight showed a fluctuating trend over the stages observed. The berries of Panniyur 1 accumulated significantly more dry weight than Karimunda. The percentage increase in dry weight to the total dry weight accumulated also differed significantly among the stages. Maximum dry weight development in Karimunda was recorded between 45-75 days while this was between 150-180 days in Panniyur 1. The development of dry weight did not show much variation between 60-135 days in the case of Karimunda. However, there was a steady increase of dry weight from 75 to 150 days in Panniyur 1 after which this shot up and then abruptly declined.

The development of berry volume also showed a trend similar to that of fresh weight in both the varieties. The final berry volume was significantly higher in Panniyur 1(14.15 cc) than Karimunda (9.84 cc). The maximum increase in volume was between 45-60 days (20.93 %) in Panniyur 1, while it was between 60-75 days (20.90 %) in the case of Karimunda. In general, more than 75 per cent of the total volume of berries was achieved within 90 days after berry set. After 90 days, the rate of increase in berry volume showed a declining trend in Karimunda. Though a similar trend was seen in Panniyur 1 also during this period, the rate of development showed an increase during 135-165 days. Much variation was not seen in berry volume after 180 days in both Karimunda and Panniyur 1.

4.2.3.3 Berry maturity and harvest

The results showed that there was no increase in fresh weight of berries after the period from 165 days in Karimunda and after 180 days in Panniyur 1. This was considered as the maturity index of berries in these varieties. However, dry weight continued to increase up to 180 days in Karimunda and 195 days in

Panniyur 1. So the harvest index was considered as 180 days and 195 days respectively, after berry set for Karimunda and Panniyur 1.

4.2.3.4 Duration of crop growth

The duration of the crop growth during a season from flowering to berry maturity were 210 days and 225 days respectively, in Karimunda and Panniyur 1 from flowering to berry maturity. Thus Karimunda matures two weeks earlier, indicating that the maturity period is at least three weeks late in Panniyur 1 as flowering was noticed a week earlier in this variety.

4.2.4. Extension growth of laterals

The growth in length of the lateral after flushing was observed at weekly interval and presented in table 13 and fig. 9a-b. The completion of extension growth in a lateral during a season required approximately 13 weeks in both the varieties. The rate of extension growth differed significantly between varieties at different stages observed. The extension growth of lateral was significantly higher in Karimunda (19.46cm) compared to Panniyur 1 (14.75cm). The maximum of extension growth occurred between 5th and 7th week in both Karimunda and Panniyur 1. The maximum rate of extension growth was during 6th week in Karimunda. The extension growth of laterals in general was exponential till the 7th week in both the varieties. After 7th week, the growth rate gradually declined and after 10th week the increase in length was less than two per cent.

About 90 per cent of the extension growth took place within 9 weeks of flushing and almost 99 per cent of the extension growth were completed within the 13th week itself in both the varieties.

The extension growth in a lateral was mediated further with leaf and spike production during its course of development. Extension growth also occurred through lateral buds in the axils of older leaves resulting in sylleptic branching (plate 12).

Plate 10a. Synchronous growth of leaf, spike and internode in Karimunda

Plate 10b. Synchronous growth of leaf, spike and internode in Panniyur 1

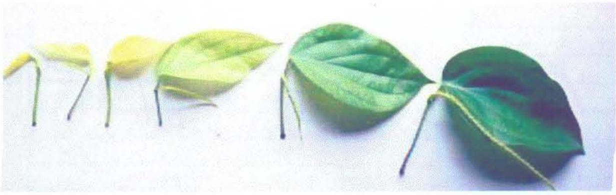


Plate 11. Initiation of growth from different nodes of a lateral

Plate 12. Sylleptic branching in black pepper

Table 13. Extension growth of laterals in black pepper

Week	Growth of laterals (cm)		Increase in length (cm)		% increase in length	
	KM	P1	KM	P1	KM	P1
1	0.45	0.47	0.45	0.47	2.34	3.17
2	1.24	1.14	0.76	0.67	6.21	5.42
3	2.41	2.24	1.23	1.07	12.33	15.17
4	4.23	3.69	1.79	1.50	21.89	25.06
5	6.63	5.74	2.49	2.09	34.02	39.07
6	9.76	8.36	3.13	2.51	50.08	57.57
7	13.29	10.79	3.45	2.51	68.15	73.49
8	15.80	12.54	2.58	1.80	81.03	85.32
9	17.19	13.63	1.81	1.03	89.12	92.50
10	18.46	14.26	0.84	0.62	94.75	96.72
11	19.00	14.59	0.50	0.34	97.57	98.87
12	19.17	14.69	0.25	0.12	98.50	99.62
13	19.41	14.74	0.15	0.29	99.71	99.93
14	19.46	14.75	0.06	0.03	100.00	100.00
CD	** 2.13		**0.442		—	

Fig. 9a Extension growth of lateral in black pepper

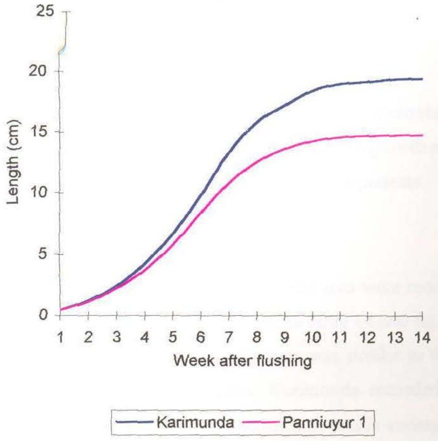
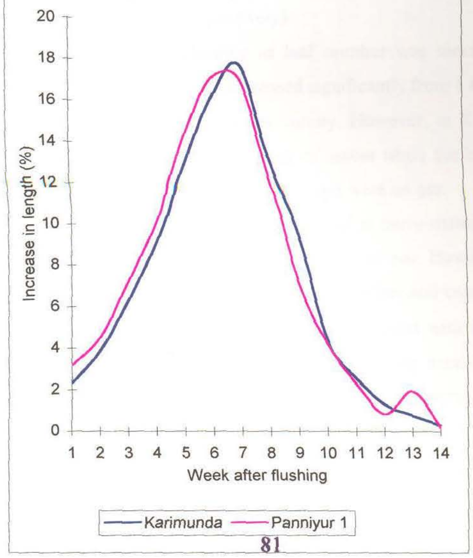


Fig. 9b Rate of growth of laterals



4.3 Morphological parameters

The morphological characters of the laterals after berry maturity and the yield parameters and productivity of the plants at harvest were studied and the results are presented hereunder:

4.3.1. Characters of lateral at berry maturity

After berry maturity, the selected laterals were separated from each canopy level of the plants and they were observed for various growth and yield characters and accumulation of fresh and dry matter in the components.

4.3.1.1 Number of leaves and leaf area

The number of leaves and average leaf area were recorded and leaf area per lateral was worked out and is presented in table 14 and fig. 10a-b.

The trend in the production of leaves was similar to that observed in the tagged laterals for the growth studies. Karimunda recorded a higher average number of leaf (3.65) while this was significantly less in variety Panniyur 1 (1.93). However, the average leaf area and leaf area per lateral were significantly higher in Panniyur 1 (99.20 cm^2 and 201.37 cm^2, respectively) compared to Karimunda (47.30 cm^2 and 179.11 cm^2, respectively).

The canopy level difference in leaf number was more pronounced in Panniyur 1. The number of leaves increased significantly from 1.66 in the lower to 2.12 in the upper canopy level in this variety. However, in Karimunda, lower canopy level recorded maximum number of leaves while the leaf production in middle and upper canopy levels were lesser and were on par.

It was observed that leaf area per lateral at berry maturity was higher in Panniyur 1 than Karimunda but was statistically on par. However, the leaf area differed significantly in the interaction between variety and canopy. Average leaf area and leaf area per lateral showed a declining trend with increasing canopy levels in Karimunda, with the lower canopy recording maximum leaf area. In Panniyur 1, the trend was reverse, with the upper canopy recording more individual leaf area and total leaf area per lateral.

Table 14. Growth characters of lateral at berry maturity

Canopy	Number of leaves		Average leaf area (cm^2)		Leaf area per lateral (cm^2)		Length of lateral (cm)		Number of nodes		Internodal length(cm)	
	KM	P1	KM	P1	KM	P1	KM	P1	KM	P1	KM	P1
Lower	3.94	1.66	53.10	98.65	215.96	173.09	22.35	13.01	4.51	2.47	5.10	5.35
middle	3.42	2.05	46.42	93.72	164.76	196.16	19.41	15.97	3.88	2.85	5.16	5.70
upper	3.60	2.12	42.40	105.23	156.61	234.86	18.30	16.53	4.08	2.86	4.56	6.01
CD	* 0.498		NS		** 56.7		** 0.2.79		**0.555		* 0.697	
Average	**3.65**	**1.93**	**47.30**	**99.20**	**179.11**	**201.37**	**20.02**	**15.17**	**4.16**	**2.72**	**4.94**	**5.69**
CD	** 0.378		** 8.95		NS		**1.61		**0.320		**0.528	

Table 15. Yield characters of lateral at berry maturity

Canopy	Number of spikes		100 berry weight (g)		100 berry volume (cc)	
	KM	P1	KM	P1	KM	P1
Lower	1.59	0.85	10.64	13.41	9.70	12.12
Middle	1.69	1.08	10.94	13.83	9.70	12.15
Upper	1.86	1.37	11.21	14.37	9.78	13.13
CD	NS		NS		* 0.542	
AV	**1.71**	**1.08**	**10.3**	**13.87**	**9.78**	**12.47**
CD	** 0.237		** 0.551		** 0.411	

Characters of the lateral at berry maturity

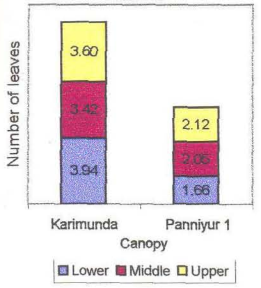


Fig. 10a Leaf productin in the laterals

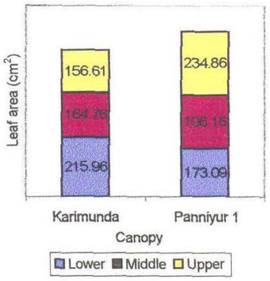


Fig. 10b Leaf area of the laterals

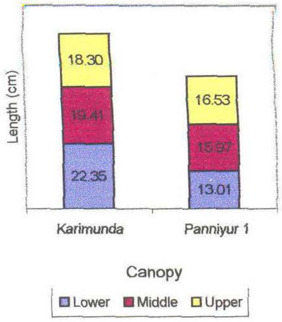


Fig. 10c Length of laterals

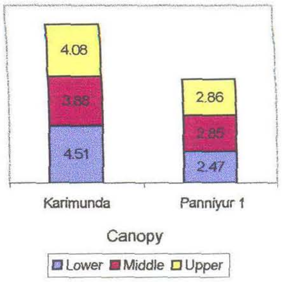


Fig. 10d Number of nodes in the laterals

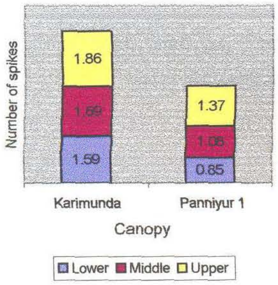


Fig. 11a Spike production in the lateral

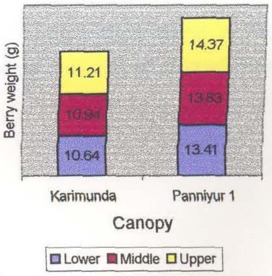


Fig. 11b Hundred berry weight

Even though the variety Karimunda produced more number of leaves in a lateral during the season, the average and total leaf area were higher in Panniyur 1.

4.3.1.2 Stem length, number of nodes and internodal length

The length, number of nodes and internodal length of the lateral at berry maturity are presented in table 14 and fig. 10c-d.

The results coincided with those obtained in the extension growth studies in tagged laterals. The current season growth in stem length of laterals differed significantly between varieties. The length of the current growth in the laterals was found to be significantly more in Karimunda, (20.02 cm), compared to Panniyur 1 (15.17 cm.)

The canopy levels differed significantly within varieties. The length of laterals was significantly more in Karimunda in the lower canopy level. It was also noted that in Karimunda, the laterals produced were shorter as the canopy levels increased, while a reverse trend was visible in Panniyur 1 as the length of laterals increased towards upper canopy levels.

The number of nodes was more in the laterals of Karimunda (4.16) while this was significantly less in Panniyur 1 (2.72). The number of nodes among canopy levels differed significantly in Karimunda and was higher in the lower canopy. However, the number of nodes was on par among the canopy levels in Panniyur 1.

The internodal length was significantly higher in Panniyur 1 (5.69 cm) as compared to Karimunda (4.94 cm). The internodal length also differed significantly among the interaction between variety and canopy. The lower and middle canopies were on par but significantly higher to upper canopy with respect to internodal length in Karimunda. In Panniyur 1, all the canopy levels were on par. While the internodal length decreased with increasing canopy levels in Karimunda, there was an increasing trend in internodal length towards upper canopy levels in Panniyur 1.

4.3.1.3 Number of spikes per lateral

The number of spikes produced per lateral also was significantly higher in Karimunda at all canopy levels (table 15 and fig. 11a). The interaction between variety and canopy did not differ significantly for the production of spikes. The spike production per lateral increased with increasing canopy level both in Karimunda and Panniyur 1, the effect being more pronounced in Panniyur 1.

4.3.1.4 Berry weight and volume

The hundred berry weight and volume were recorded at berry maturity and the results obtained were similar to those obtained in the study for the development of berry weight and volume. Berry weight and volume were significantly higher in Panniyur 1 (13.87 g and 12.47 cc respectively) than Karimunda (10.30 g and 9.78 cc respectively) (table15 and fig. 11b).

4.3.2. Fresh and dry matter accumulation and partitioning in the lateral

The data on fresh weight and dry matter accumulation in the components of the lateral such as shoot, leaf and spike and the total weight of lateral are presented in table 16 and 17.

4.3.2.1 Accumulation in the stem

The stem fresh weight and dry weight differed significantly between varieties. The fresh weight of the stem was significantly more in Panniyur 1 (2.41 g/ lateral) than Karimunda (1.65 g/lateral).

The interaction between variety and canopy levels also differed significantly for both parameters. In Panniyur 1, the canopy levels were significantly different and the stem fresh weight was highest (2.97 g/ lateral) in the upper canopy, which was on par with middle canopy. However, in Karimunda, stem fresh weight was on par at all the canopy levels. In general, fresh and dry weight of stem showed an increasing trend with increasing canopy level, with the upper canopy registering the highest fresh and dry weights.

Table 16. Accumulation of bio-mass in the laterals at berry maturity

Canopy	Fresh weight (g)								Dry weight (g)									
	Stem		Leaf		Spike		Total		Stem		Leaf		Spike		Total		per cm	
	KM	P1	KM	P1	KM	P1	KM	P1	KM	P1	KM	P1	KM	P1	KM	P1	KM	P1
Lower	1.60	1.76	5.33	4.81	3.14	6.87	10.07	14.47	0.349	0.331	1.176	0.929	0.762	1.758	2.337	3.016	0.02	0.03
Middle	1.63	2.51	4.46	5.70	4.06	9.09	10.44	18.77	0.341	0.487	0.966	1.103	1.052	2.368	2.359	3.958	0.02	0.03
Upper	1.72	2.97	4.24	6.49	3.90	11.19	9.85	21.05	0.369	0.533	0.922	1.209	1.055	2.972	2.377	4.712	0.02	0.03
CD	* 0.580		** 1.27		** 2.11		** 3.13		NS		**0.240		*0.421		**0.70		NS	
Average	**1.65**	**2.41**	**4.68**	**5.67**	**3.70**	**9.05**	**10.12**	**18.09**	**0.353**	**0.451**	**1.021**	**1.080**	**0.956**	**2.366**	**2.358**	**3.895**	**0.02**	**0.03**
CD	** 0.447		** 0.731		**1.22		** 1.91		** 0.094		NS		**0.320		** 0.404		NS	

Table 17. Partitioning of fresh weight and dry weight and dry weight percentage of the components of the lateral

Canopy	Fresh weight partitioning (%)						Dry weight partitioning (%)						Dry weight percentage					
	stem		leaf		spike		stem		leaf		spike		stem		Leaf		Spike	
	KM	P1	KM	P1	KM	P1	KM	P1	KM	P1	KM	P1	KM	P1	KM	P1	KM	P1
Lower	16.39	12.38	53.85	34.26	29.75	48.25	15.33	10.69	51.15	31.05	33.21	57.46	21.93	18.58	22.1	19.63	26.23	25.35
Middle	16.08	13.56	43.70	32.07	36.92	49.28	15.13	11.55	43.10	28.81	41.27	57.61	21.13	18.55	21.8	19.16	24.28	26.16
Upper	17.51	14.00	43.63	31.25	38.85	53.32	15.76	11.29	41.04	26.41	42.68	62.31	21.59	18.45	22.7	19.19	26.94	25.89
CD	NS		NS		NS		NS		NS		NS		NS		NS		NS	
AV	**16.66**	**13.30**	**47.06**	**32.53**	**35.17**	**50.28**	**15.41**	**11.18**	**45.10**	**28.76**	**39.06**	**59.13**	**21.55**	**18.53**	**22.2**	**19.33**	**25.82**	**25.80**
CD	** 2.13		** 4.14		** 3.97		** 2.21		** 4.47		** 5.44		**0.931		* 1.17		NS	

Dry weight of stem was significantly higher in Panniyur 1 compared to Karimunda. The canopy levels were not significant for stem dry weight. The dry weight per unit length of lateral did not differ significantly between varieties. However, unit dry weight was more in Panniyur 1 (0.03 g/cm) compared to Karimunda (0.02 g/ cm). Both Karimunda and Panniyur 1 showed increasing dry weight content per unit length as the canopy level increased.

The stem dry weight percentage was significantly higher in Karimunda (21.55 %) than Panniyur 1 (18.53 %). However, the canopy level differences were not significant (table 17).

4.3.2.2 Accumulation in leaf

The leaf fresh weight per lateral also differed significantly between varieties (table16). Panniyur 1 recorded higher fresh weight (5.67 g) compared to Karimunda (4.68 g). The interaction between variety and canopy also was significant. While the leaf fresh weight showed a decreasing trend towards upper canopy levels in Karimunda, a reverse trend was observed in Panniyur 1.

The leaf dry weight was not significantly different between varieties. However, the interaction between variety and canopy was significant. The leaves from lower canopy accumulated significantly more dry weight (1.176 g) compared to upper canopy (0.922 g) in Karimunda. In Panniyur 1, the upper canopy leaves recorded significantly higher dry weight (1.209 g).

Dry weight percentage of leaves was significantly higher in Karimunda (22.23 %) than Panniyur 1(19.33 %) (table17). The canopy level variations were not significant for dry weight percentage of leaf.

4.3.2.3 Accumulation in spikes

The spike fresh weight differed significantly between varieties. Panniyur 1 accumulated a higher fresh spike weight per lateral at all the canopy levels. Spike fresh weight was also significant among canopy levels. Panniyur 1 recorded significantly higher spike fresh weight in both middle and upper canopy levels. The maximum fresh weight of 11.19 g was recorded in Panniyur 1 at the upper canopy level. The berry fresh weights recorded at all canopy levels were on par in Karimunda.

Spike dry weight also was significantly higher in Panniyur 1 compared to Karimunda. This character differed significantly in the interaction between variety and canopy level as well. The spike dry weight varied significantly among canopy levels in Panniyur 1 wherein the upper canopy registered the maximum value of 2.972 g followed by middle (2.638 g) and lower (1.758 g) canopy levels. In Karimunda, canopy levels were on par.

There was no significant difference in the dry weight percentage of spikes in Panniyur 1 and Karimunda (table 17). The canopy levels were not significantly different for dry weight percentage of spike as well.

4.3.2.4 Total accumulation in the laterals

The total fresh weight of the laterals showed a similar trend as that of its components (fig. 12a). The total fresh biomass produced during the current season growth of the lateral was 18.09 g in Panniyur1 while it was only 10.12 g in Karimunda.

The total fresh weight of the lateral also differed significantly among canopy levels. The total biomass showed an increasing trend towards upper canopy levels in Panniyur 1. The maximum fresh weight was recorded by the upper canopy level (21.05 g). In Karimunda, the canopy levels were on par.

The total dry weight of the lateral also was significant between varieties, among canopy levels and their interaction (fig. 12b). The total dry weight of the lateral was significantly higher in Panniyur 1 (3.895 g) than Karimunda (2.358 g). The total dry weight was higher at all the canopy levels in Panniyur 1 compared to Karimunda. The total dry weight was the maximum in the upper canopy level in Panniyur 1.

Accumulation and partitioning of biomass in the laterals

Fig. 12a Total fresh weight accumulation in laterals

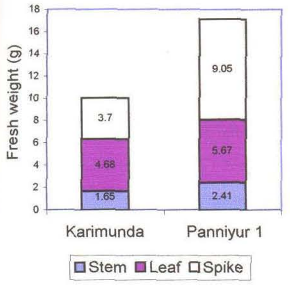


Fig. 12b Dry weight accumulation in laterals

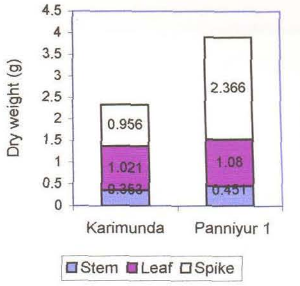


Fig. 13a Fresh weight partitioning in Karimunda

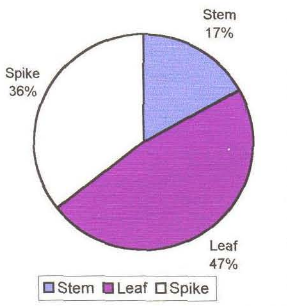


Fig. 13b Fresh weight partitioning in Panniyur 1

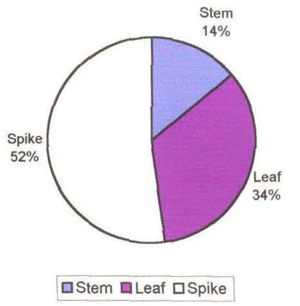


Fig. 14a Dry weight partitioning in Karimunda

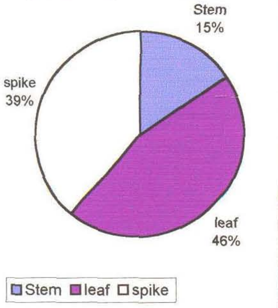
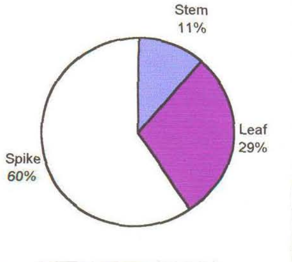


Fig. 14b Dry weight partitioning in Panniyur 1



4.3.2.5 Fresh and dry weight partitioning in laterals

The percentage partitioning of the fresh and dry matter into various component organs of the laterals such as stem, leaf and berry were analysed and presented in table 17 and fig. 13a-14b.

The partitioning of biomass among the different components showed that in Karimunda, maximum biomass was partitioned to leaves (47.06 %), while in Panniyur 1, maximum biomass was partitioned to spikes (50.28 %).

Partitioning of fresh biomass into leaf was significantly higher in Karimunda (47.06 %) than Panniyur 1 (32.52 %). In Karimunda, the lowest canopy recorded maximum partitioning of fresh weight in leaf (53.85 %). Though not significant, partitioning of biomass to leaf showed negative trend with increasing canopy level in both the varieties.

The variation in partitioning of dry matter to leaf also was significant between varieties. The partitioning of dry matter by leaf was significantly higher in Karimunda (45.10 %) than Panniyur 1 (28.76 %). The interaction between variety and canopy level was not significantly different for partitioning by leaves.

The partitioning of stem fresh and dry matter was significantly higher in Karimunda (16.66 % and 15.41 %, respectively) than Panniyur 1 (13.30 % and 11.18 % respectively). However, there was no significant variation in canopy level partitioning by stem.

The partitioning of spike fresh matter was significantly higher in Panniyur 1 (50.28 %) than Karimunda (35.17 %). However, the canopy levels were not significantly different for partitioning of fresh matter. The fresh matter partitioning to berries showed a linear increase with increasing canopy levels in both Karimunda and Panniyur 1.

The partitioning of dry matter to spikes was also significantly different between varieties. The partitioning to spikes was significantly higher in Panniyur 1 (59.13 %) than Karimunda (39.06 %). The variety x canopy interaction was not significantly different. However, the dry weight partitioning by spikes increased from lower to upper canopy levels.

4.3.3 Spike and yield characters of the plant at harvest

The spike and berry characters such as the length of spike, spike weight, dry weight percentage of berries, number of developed, undeveloped, pollu affected and total number of berries per spike were recorded at the time of harvest and presented in table 18 and fig. 15a-d.

It was observed that spike length, spike weight, number of developed berries and total number of berries per spike were significantly higher in the variety Panniyur 1 compared to Karimunda. The dry weight percentage was on par in both the varieties. Panniyur 1 recorded a spike length of 10.09 cm while it was 7.20 cm in Karimunda. The weight of individual spike was 7.15 g and 3.49 g respectively in Panniyur 1 and Karimunda. The number of developed and total number of berries per spike in Panniyur 1 were 45.76 and 58.59 respectively, while these were only 26.23 and 29.37 respectively, in Karimunda.

The canopy level variation in characters such as developed berries and total berries per spike was evident, as these were significantly higher in the upper canopy in Panniyur 1. Spike length also was significantly high in the upper canopy in both the varieties.

The yield characters and dry pepper yield of the plants were also recorded at the time of harvest and presented in table 19 and fig. 16a-d.

The number of spikes, spike fresh weight, and green and dry pepper yield differed significantly between varieties. The number of spikes was significantly higher in Karimunda (1820.05) compared to Panniyur 1 (859.35). However, the total spike weight as well as green and dry pepper yield per plant was significantly higher in Panniyur 1. Green and dry pepper yield were 5911.50g and 1958.00 g respectively, in Panniyur 1 while these were 4611.85 and 1517.14 respectively, in Karimunda.

The effect of canopy level followed similar trend in both the varieties. Number of spikes, fresh spike and berry weight and dry pepper yields were higher in the upper canopy level. The middle and top canopies were more productive especially in the variety Panniyur 1. The dry pepper yield also was more in the upper canopy in both the varieties.

Table 18. Spike and berry characters of black pepper varieties

Canopy	spike length (cm)		Spike weight (g)		Dry weight (%)		Number of berries per spike							
							Developed		Undeveloped		Pollu affected		Total	
	KM	P1	KM	P1	KM	P1	Km	P1	KM	P1	KM	P1	KM	P1
Lower	6.70	9.13	3.07	6.26	32.30	31.79	24.26	38.27	3.20	3.18	0.14	1.04	27.62	44.50
Middle	7.32	9.90	3.49	7.21	32.99	33.04	25.58	44.73	2.63	3.02	0.28	1.07	28.49	48.86
Upper	7.64	11.23	3.91	7.99	33.50	33.87	28.87	54.29	2.91	2.82	0.23	1.23	31.99	58.41
CD	** 0.682		NS		NS		** 5.72		NS		NS		** 5.58	
Average	**7.20**	**10.09**	**3.49**	**7.15**	**32.93**	**32.90**	**26.23**	**45.76**	**2.92**	**3.01**	**0.22**	**1.11**	**29.37**	**58.59**
CD	** 0.518		** 0.532		NS		** 3.30		NS		** 0.376		** 3.22	

Table 19. Yield characters and dry pepper yield of black pepper varieties

canopy	Number of spikes		Spike fresh weight (g)		Berry green weight (g)		Dry pepper yield (g)	
	KM	P1	KM	P1	KM	P1	Km	P1
Lower	422.95	153.90	1006.50	994.50	942.55	896.50	304.25	255.95
Middle	638.10	261.55	1851.00	2015.40	1640.30	1772.20	542.09	604.95
Upper	759.00	443.90	2515.15	3596.25	2029.00	3242.80	670.80	1097.10
CD	** 141.77		* 617.72		** 632.20		** 209.09	
Total	**1820.05**	**859.35**	**5372.65**	**6606.15**	**4611.85**	**5911.50**	**1517.14**	**1958.00**
CD	** 360.52		* 1115.43		* 1227.26		* 405.11	

Spike and berry characters in black pepper at berry maturity

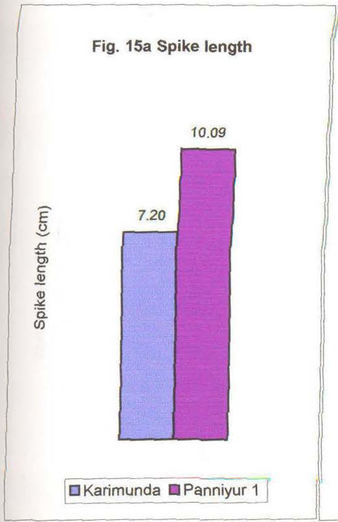


Fig. 15a Spike length

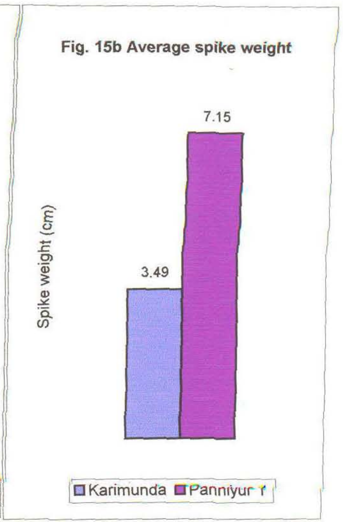


Fig. 15b Average spike weight

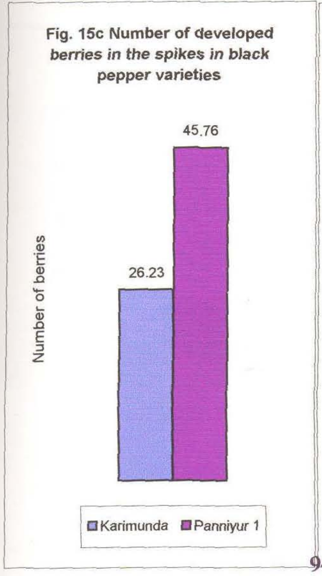


Fig. 15c Number of developed *berries in the spikes in black pepper varieties*

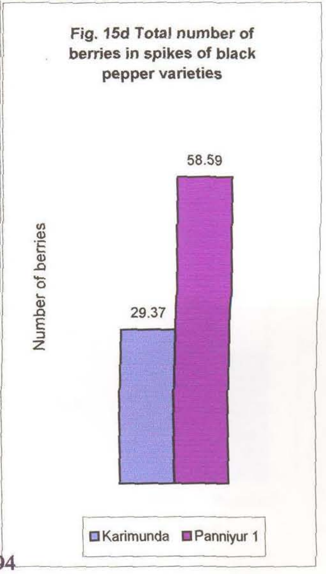


***Fig. 15d* Total number of berries in spikes of black pepper varieties**

Yield characters of the vine at harvest in black pepper varieties

Fig. 16a Spike production

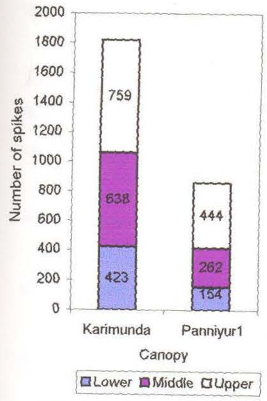


Fig. 16b Fresh yield of spikes

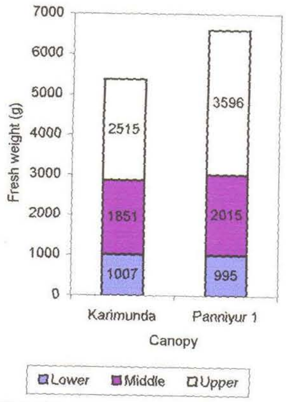


Fig. 16c Yield of fresh berries

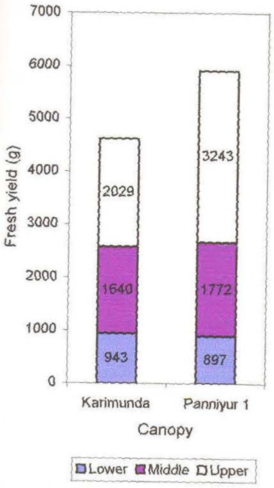
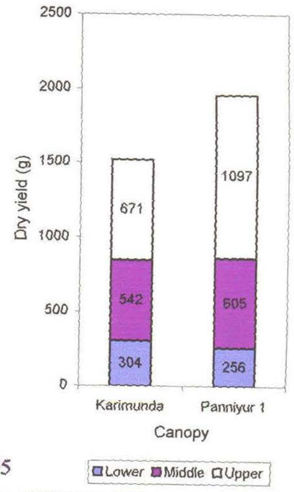


Fig. 16d Dry pepper yield



4.4 Physiological parameters

The physiological parameters such as specific leaf weight, specific leaf area, specific gravity of berries, leaf weight ratio and spike to leaf ratio which were derived from the data collected from the morphological observations are presented in table 20.

4.4.1 Specific leaf area

The specific leaf area did not differ significantly between Karimunda and Panniyur 1. The specific leaf area was the maximum in the lower canopy level in Karimunda. In Panniyur 1, the specific leaf area was the maximum at the upper canopy while this was minimum at middle canopy in both the varieties.

4.4.2 Specific leaf weight

The specific leaf weight, which is leaf dry weight per unit leaf area, did not show any significant variation between varieties and among canopy levels.

4.4.3 Leaf weight ratio

The leaf weight ratio was significantly high in Karimunda (0.44) compared to Panniyur 1 (0.28). The leaf weight ratio showed a decreasing trend with increasing canopy level in both the varieties. The leaf weight ratio was highest at the lower canopy levels in both Karimunda and Panniyur1.

4.4.4 Specific gravity of berries

There is uniform development of berry fresh weight and volume resulting a specific gravity around one. The specific gravity of berries did not differ significantly between varieties and stages.

4.4.5 Spike to leaf ratio

The variety Karimunda recorded a higher spike to leaf ratio (0.72) compared to Panniyur 1 (0.70). Among the canopy levels, highest spike to leaf ratio was recorded by Panniyur 1 in the upper canopy (0.754). The spike to leaf

Table 20. Physiological parameters in black pepper at berry maturity

Canopy	Specific leaf weight (mg/cm^2)		Specific leaf area (cm^2/g)		Specific gravity of berries		Leaf weight ratio		Spike to leaf ratio	
	KM	**P1**	**KM**	**P1**	**KM**	**P1**	**KM**	**P1**	**KM**	**P1**
Lower	0.01	0.01	178.18	176.18	1.10	1.10	0.50	0.31	0.716	0.61
Middle	0.01	0.01	164.62	170.40	1.12	1.40	0.41	0.28	0.696	0.672
Upper	0.01	0.01	165.61	184.61	1.15	1.10	0.40	0.26	0.745	0.754
Average	**0.01**	**0.01**	**169.47**	**177.06**	**1.12**	**1.20**	**0.44**	**0.28**	**0.72**	**0.68**
CD	NS		NS		NS		** 0.11		* 0.014	

ratio recorded by middle and upper canopies were on par between varieties, while the spike to leaf ratio was significantly higher in Karimunda in the lower canopy.

4.5 Gas exchange parameters

4.5.1 Leaf photosynthesis

The leaf photosynthetic rate (A) was measured under ambient condition by using a portable photosynthetic system and presented in table 21 and fig. 17a-b.

The average leaf photosynthetic rate per unit area differed significantly between varieties. Panniyur 1 recorded a photosynthetic rate of 2.001 μmol $m^{-2} s^{-1}$ while this was 1.842 μmol $m^{-2}s^{-1}$ for Karimunda. The photosynthetic rate did not differ significantly for variety x canopy interaction. The upper canopy recorded highest average photosynthesis compared to the lower canopy in both the varieties. The rate of photosynthesis increased towards middle and upper canopy levels.

Among the various stages observed, the first and third fortnight after flushing recorded the maximum photosynthetic rate in both Karimunda and Panniiyur 1. These periods coincided with flushing, flowering, and berry set. Thereafter the photosynthetic rate showed a fluctuation till maturity. This trend was similar in both the varieties.

Spike bearing lateral showed significantly high photosynthetic rate during all the stages observed in both Karimunda and Panniyur 1. The photosynthetic rate was almost double (2.575 μmol $m^{-2}s^{-1}$) in spike bearing laterals as compared to laterals without spike (1.269 μ mol $m^{-2}s^{-1)}$.

4.5.2 Stomatal resistance (r_s)

The stomatal resistance also differed significantly between varieties (table 22 and fig. 18a-b). The stomatal resistance was high in Karimunda (229.99 m^2 s mol $^{-1}$) than Panniyur 1 (200.98 m^2 s mol $^{-1}$). The stomatal resistance also was highly fluctuating and differed significantly among the stages observed in both the varieties. However, the stomatal resistance was lower during the later stages, as it advanced towards berry maturity. In variety Panniyur 1, the highest stomatal

Table 21. Leaf photosynthetic rate (μmol m^{-2} s^{-1}) at various developmental stages of the laterals in black pepper

Stages	Canopy								Lateral					
	Lower		Middle		Upper		Average		With out spike		With spike		Average	
	KM	P1	KM	P1	KM	P1	KM	P1	KM	P1	KM	P1	Without spike	With spike
Flushing & flowering	1.813	1.934	3.894	3.701	4.655	4.828	**3.458**	**3.487**	1.873	2.030	5.040	4.945	**1.951**	**4.994**
Spike development	1.581	1.979	1.383	2.325	2.436	2.524	**1.800**	**2.276**	1.124	1.503	2.477	3.049	**1.313**	**2.763**
Berry set	1.721	3.373	2.354	2.983	2.160	2.949	**2.078**	**3.102**	1.240	1.868	2.916	4.335	**1.554**	**3.626**
Early berry development	1.970	1.425	2.280	1.744	1.797	1.635	**2.016**	**1.601**	1.107	0.941	2.925	2.262	**1.024**	**2.593**
Late berry development	1.040	0.880	0.833	0.660	1.064	0.816	**0.979**	**0.785**	0.612	0.604	2.346	0.967	**0.608**	**1.157**
Berry maturity	1.936	1.223	1.028	1.724	1.354	1.317	**1.439**	**1.421**	1.527	0.862	1.352	1.981	**1.194**	**1.667**
Harvest	1.477	1.784	0.854	1.229	1.051	0.997	**1.127**	**1.336**	1.202	1.277	1.053	1.396	**1.239**	**1.225**
CD	NS						** 0.459		** 0.650				** 0.459	
Average	**1.648**	**1.800**	**1.804**	**2.052**	**2.074**	**2.152**	**1.842**	**2.001**	**1.241**	**1.298**	**2.587**	**2.705**	**1.269**	**2.575**
CD	NS						**0.117		NS				** 0.325	

Table 22. Stomatal resistance (m^2 s mol^{-1}) of leaves at various developmental stages of laterals in black pepper

Stages	Canopy								Lateral					
	Lower		Middle		Upper		Average		Without spike		With spike		Average	
	KM	P1	KM	P1	KM	P1	KM	P1	KM	P1	KM	P1	Without spike	With spike
Flushing & flowering	196.76	386.15	242.68	374.01	188.84	285.99	**209.43**	**348.72**	215.80	358.44	203.06	339.00	**209.43**	**348.72**
Spike development	255.00	204.21	225.39	211.37	221.89	201.25	**234.09**	**205.61**	238.32	184.24	229.57	226.99	**234.09**	**205.62**
Berry set	396.56	179.44	275.53	186.12	229.42	165.20	**300.50**	**176.92**	309.20	169.74	291.80	184.09	**300.50**	**176.92**
Early berry development	260.81	221.59	259.49	217.87	246.68	194.50	**255.66**	**163.89**	258.67	208.67	252.44	213.97	**255.66**	**211.32**
Late berry development	196.02	161.70	221.41	200.48	192.91	167.50	**203.45**	**176.56**	202.58	174.14	204.31	178.98	**203.45**	**176.56**
Berry maturity	210.12	171.53	210.24	192.09	211.04	167.60	**210.46**	**177.08**	214.18	179.72	206.75	174.44	**210.46**	**177.08**
Harvest	213.29	164.83	203.65	158.11	172.17	151.34	**196.37**	**158.09**	200.59	158.65	192.15	157.53	**196.37**	**158.09**
CD	** 47.05						** 15.68		NS				** 27.16	
Average	**246.94**	**212.78**	**234.06**	**220.01**	**208.99**	**190.48**	**229.99**	**200.98**	**234.19**	**204.80**	**225.73**	**210.71**	**229.99**	**207.76**
CD	NS						** 9.05		NS				** 9.05	

Gas exchange parameters at various stages of development in black pepper

***Fig. 17a* Variation in leaf photosynthetic rate (A) between varieties**

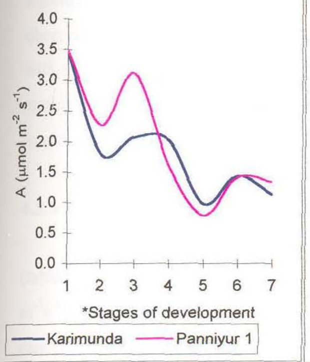


***Fig. 17b* Variation in A between the type of laterals**

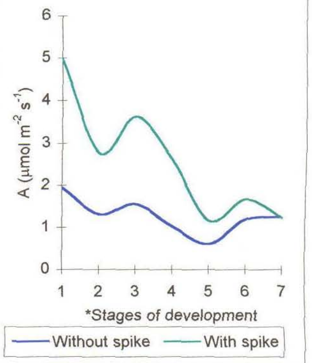


Fig. 18a Variation in stomatal resistance (r_s) of leaves between varieties

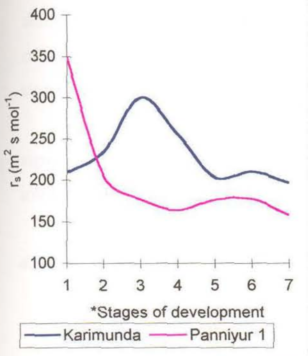
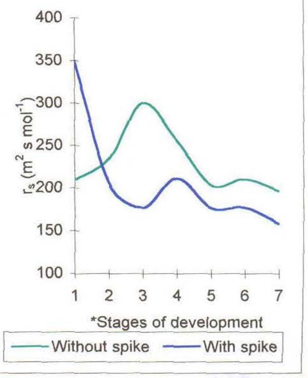


Fig. 18b Variation in r_s between the type of laterals



* 1. Flushing and flowering 2. Spike development 3. Berryset 4. Early berry development 5. Late berry development 6. Berry maturity 7.Harvest

resistance observed was during flushing and flowering stage, which coincided with the period of leaf area development. The stomatal resistance did not differ significantly for variety and canopy interaction. The lower canopy level recorded highest stomatal resistance in the variety Karimunda. However, in Panniyur 1, middle canopy levels recorded maximum stomatal resistance.

The stomatal resistance recorded at various stages also differed significantly between varieties and was high in Karimunda during all the stages observed except flushing and flowering. However, no definite trend was visible with the stages such as flushing and flowering, berry set, berry development and maturity. The leaves of laterals without spikes recorded higher r_s values compared to spike bearing laterals.

4.5.3 Transpiration rate

The transpiration rate of leaves differed significantly between varieties (table 23 and fig. 19a-b). This was significantly high in Panniyur 1 (0.301 mol $m^{-2}s^{-1}$) compared to Karimunda (0.272 mol $m^{-2}s^{-1}$). The interaction for variety x canopy and variety x stages also differed significantly. The transpiration rate of Panniyur 1 was found high at all canopy levels compared to Karimunda. The transpiration rate fluctuated between stages and was either on par or high in the leaves of Panniyur 1 than Karimunda during all the stages except flushing and flowering. The fluctuation in transpiration rate during all the stages followed a similar pattern for both Karimunda and Panniyur 1. The highest transpiration rate of 0.407 mol $m^{-2}s^{-1}$ was observed in Panniyur 1 during early berry development stage.

The spike bearing laterals and those without spikes did not differ significantly in the transpiration rate. Panniyur 1 recorded high transpiration rate irrespective of whether the lateral was productive or not.

4.5.4 Leaf surface temperature

The leaf surface temperature differed significantly between varieties, variety x canopy levels, and variety x stages (table 24 and fig. 20a-b). Leaf surface

Table 23. Transpiration rate (mol $m^{-2}s^{-1}$) of leaves at various developmental stages in black pepper

Stages	Canopy								Lateral					
	Lower		Middle		Upper		Average		Without spike		With spike		Average	
	KM	P1	KM	P1	KM	P1	KM	P1	KM	P1	KM	P1	without spike	with spike
Flushing & flowering	0.384	0.262	0.243	0.265	0.351	0.304	**0.326**	**0.277**	0.316	0.271	0.335	0.283	**0.294**	**0.309**
Spike development	0.238	0.258	0.223	0.236	0.253	0.263	**0.238**	**0.252**	0.225	0.263	0.252	0.291	**0.244**	**0.246**
Berry set	0.300	0.297	0.228	0.293	0.275	0.329	**0.267**	**0.306**	0.262	0.308	0.273	0.305	**0.285**	**0.289**
Early berry development	0.318	0.413	0.287	0.390	0.348	0.417	**0.318**	**0.407**	0.312	0.410	0.323	0.404	**0.361**	**0.364**
Late berry development	0.214	0.250	0.205	0.184	0.247	0.226	**0.222**	**0.220**	0.209	0.216	0.235	0.224	**0.212**	**0.230**
Berry maturity	0.239	0.291	0.206	0.252	0.253	0.332	**0.233**	**0.292**	0.216	0.300	0.250	0.283	**0.258**	**0.266**
Harvest	0.299	0.364	0.255	0.334	0.339	0.361	**0.298**	**0.353**	0.297	0.359	0.298	0.347	**0.328**	**0.323**
CD	NS						** 0.024		NS				** 0.024	
Average	**0.285**	**0.305**	**0.235**	**0.279**	**0.295**	**0.319**	**0.272**	**0.301**	**0.262**	**0.304**	**0.2809**	**0.305**	**0.283**	**0.290**
CD	** 0.014						** 0.008		** 0.011				NS	

Table 24. Leaf surface temperature (^0C) at various developmental stages in black pepper

Stages	Canopy								Lateral					
	Lower		Middle		Upper		Average		Without spike		With spike		Average	
	KM	P1	KM	P1	KM	P1	KM	P1	KM	P1	KM	P1	Without spike	With spike
Flushing & flowering	28.47	29.07	27.86	28.78	28.54	29.33	**28.29**	**29.06**	28.22	29.07	28.36	29.06	**28.65**	**28.71**
Spike development	28.64	28.71	28.20	28.36	28.65	29.77	**28.50**	**28.61**	28.46	28.47	28.54	28.76	**28.46**	**28.65**
Berry set	29.34	30.30	29.41	30.15	29.81	30.42	**29.52**	**30.29**	29.33	30.06	29.71	30.52	**29.70**	**30.11**
Early berry development	31.31	34.48	31.40	34.18	32.08	34.85	**31.59**	**34.50**	31.46	34.47	31.73	34.53	**32.97**	**33.13**
Late berry development	31.76	33.92	31.91	34.12	32.42	34.40	**32.03**	**34.15**	32.00	34.08	32.06	34.21	**33.04**	**33.14**
Berry maturity	30.94	33.70	30.82	37.38	30.78	35.14	**30.85**	**34.41**	30.71	34.65	30.98	34.17	**32.68**	**32.58**
Harvest	32.42	34.62	32.74	34.48	33.60	35.03	**32.92**	**34.71**	32.98	34.89	32.87	34.54	**33.93**	**33.70**
CD	NS						0.342		NS				0.342	
Average	**30.41**	**32.11**	**30.33**	**32.49**	**30.84**	**32.71**	**30.53**	**32.25**	**30.45**	**32.24**	**30.61**	**32.26**	**31.35**	**31.43**
CD	NS						0.114		0.201				NS	

Gas exchange parameters at various stages of development in black pepper

Fig. 19a Variation in *transpration rate (E) rate of* leaves between varieties

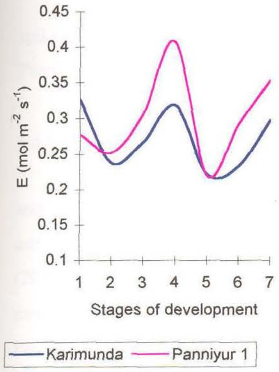


Fig. 19b Variation in E between the type of laterals

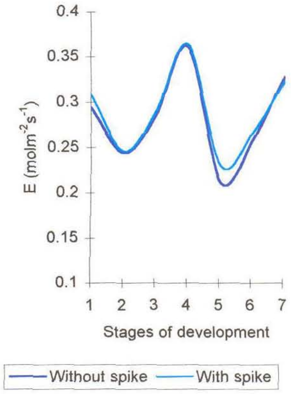


Fig.20a Variation in leaf *surface temperature* between varieties

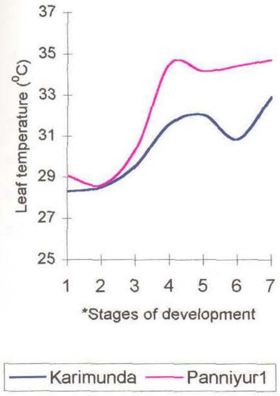
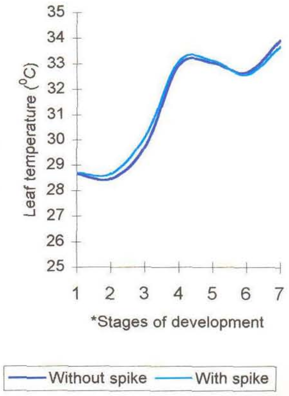


Fig. 20b Variation in leaf *surface temperature* between the type of laterals



*1. *Flushing and flowering* 2. Spike development 3. Berry set 4. Early berry development 5. Late berry development 6. Berry maturity 7. Harvest temperature recorded by Panniyur 1 (32.25 ^{0}C) was significantly higher compared to Karimunda (30.53 ^{0}C). Similar results followed at all canopy levels and stages. There was a gradual increase in leaf surface temperature as the season advanced from flowering to harvest in both Karimunda and Panniyur 1. Canopy level variation in leaf temperature was also significant and was the maximum in the upper canopy level in both Karimunda and Panniyur 1.

There was no significant difference in the leaf temperature recorded by spike bearing laterals and laterals without spikes in both Karimunda and Panniyur 1.

4.5.5 Photosyntheticallly active radiation (PAR)

The PAR received at leaf surface was measured and presented in table 25 and fig. 21a-b. The PAR differed significantly between varieties, type of laterals and stages. PAR received at leaf surface by Panniyur 1 was significantly higher (297.52 µmol m^{-2}-s^{-1}) compared to Karimunda (274.15 µmol m^{-2} s^{-1}). The upper canopy level recorded maximum PAR on leaf surface in both Karimunda and Panniyur 1. The PAR was also fluctuating among the stages and was the highest during the stage at harvest in Karimunda and early berry development in Panniyur 1.

The spike bearing laterals recorded significantly higher PAR on leaf surface compared to laterals without spikes in both Karimunda and Panniyur 1.

4.5.6 Vapour pressure deficit (VPD)

The VPD recorded by leaves differed significantly between varieties (table 26 and fig. 22a-b). VPD was significantly higher in Panniyur 1 (0.349 m bar) while it was low (0.314 m bar) in Karimunda. The canopy levels were not significantly different. However, the middle canopy level recorded the least VPD, and the upper canopy recorded the maximum in both the varieties. The VPD was highly fluctuating among the stages observed. There was no significant difference between the spike bearing and spikeless laterals in VPD recorded by leaves.

Table 25. PAR (μmol $m^{-2}s^{-1}$) at leaf surface at various developmental stages of the laterals in black pepper

Stages	Canopy								Lateral					
	Lower		Middle		Upper		Average		Without spike		With spike		Average	
	KM	P1	KM	P1	KM	P1	KM	P1	KM	P1	KM	P1	Without spike	With spike
Flushing & flowering	227.53	199.40	259.40	255.70	300.53	322.00	**262.49**	**259.03**	237.27	221.76	287.71	296.31	**229.51**	**292.01**
Spike development	267.10	216.07	243.93	236.00	276.17	259.60	**259.40**	**237.22**	249.53	220.87	269.27	253.58	**235.20**	**261.42**
Berry set	296.93	315.73	270.60	316.83	279.07	302.00	**282.20**	**311.52**	276.33	294.89	288.07	328.16	**285.61**	**308.11**
Early berry development	284.70	328.40	288.63	325.30	275.87	386.83	**284.73**	**346.85**	277.87	342.38	301.60	351.31	**310.12**	**326.46**
Late berry development	246.20	286.77	250.83	255.50	269.87	288.07	**255.63**	**276.78**	245.33	274.92	265.93	278.64	**260.12**	**272.29**
Berry maturity	255.10	296.40	286.64	324.97	290.00	326.30	**277.24**	**315.89**	272.89	322.42	281.60	309.36	**297.66**	**295.48**
Harvest	303.10	364.37	285.83	309.47	303.17	332.27	**297.37**	**335.37**	298.71	336.87	296.02	333.87	**317.79**	**314.94**
CD	** 34.47						** 19.9		NS				** 19.90	
Average	**268.67**	**286.73**	**269.41**	**289.11**	**284.95**	**316.72**	**274.15**	**297.52**	**265.42**	**287.73**	**284.31**	**307.32**	**276.57**	**295.82**
CD	NS						** 6.63		NS				** 6.63	

Table 26. VPD (m bar) at various developmental stages of the laterals in black pepper

Stages	Canopy								Lateral					
	Lower		Middle		Upper		Average		Without spike		With spike		Average	
	KM	P1	KM	P1	KM	P1	KM	P1	KM	P1	KM	P1	Without spike	With spike
Flushing & flowering	0.344	0.250	0.223	0.249	0.346	0.292	**0.304**	**0.264**	0.295	0.263	0.313	0.264	**0.279**	**0.289**
Spike development	0.261	0.276	0.221	0.236	0.261	0.279	**0.247**	**0.263**	0.247	0.275	0.248	0.252	**0.261**	**0.250**
Berry set	0.358	0.374	0.352	0.365	0.380	0.409	**0.363**	**0.382**	0.368	0.388	0.359	0.377	**0.378**	**0.368**
Early berry development	0.350	0.420	0.345	0.409	0.353	0.433	**0.349**	**0.421**	0.349	0.418	0.350	0.423	**0.384**	**0.386**
Late berry development	0.297	0.306	0.310	0.335	0.322	0.300	**0.310**	**0.314**	0.311	0.301	0.309	0.327	**0.306**	**0.318**
Berry Maturity	0.271	0.340	0.262	0.388	0.271	0.360	**0.268**	**0.362**	0.240	0.391	0.296	0.334	**0.315**	**0.315**
Harvest	0.383	0.452	0.324	0.420	0.374	0.429	**0.360**	**0.437**	0.369	0.465	0.352	0.402	**0.417**	**0.377**
CD	NS						** 0.048		NS				** 0.049	
Average	**0.323**	**0.345**	**0.291**	**0.343**	**0.330**	**0.357**	**0.314**	**0.349**	**0.311**	**0.357**	**0.318**	**0.340**	**0.334**	**0.329**
CD	NS						** 0.016		NS				NS	

Gas exchange parameters at various stages of development in black pepper

Fig. 21a Variation in photosynthetically active radiations (PAR) between varieties

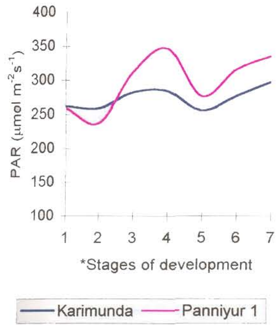


Fig. 21b Variation in PAR between the type of laterals

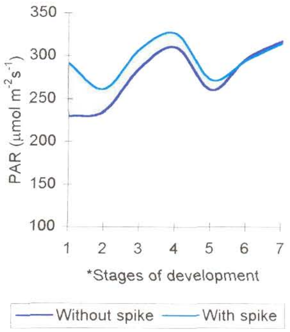


Fig. 22a Variation in vapour pressure deficit (VPD) between varieties

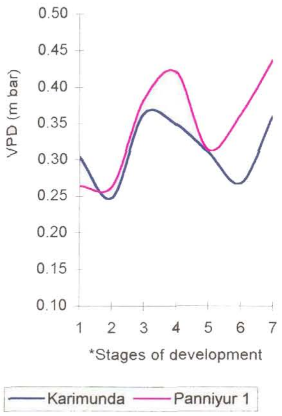
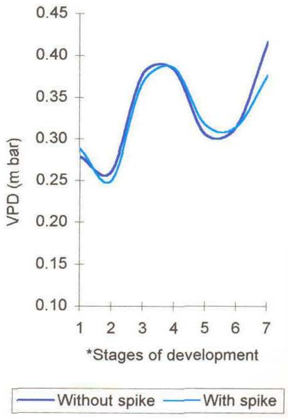


Fig. 22b Variation in VPD between the type of laterals



*1. Flushing and flowering 2. Spike development 3. Berry set 4. Early berry development 5. Late berry development 6. Berry maturity 7. Harvest

4.5.7 Stomatal conductance (g_s)

The stomatal conductance also differed significantly between varieties at 5.0 per cent level (table 27 and fig. 23a-b). Stomatal conductance recorded by leaves in Panniyur 1 was higher (0.130) than Karimunda (0.118). The interaction between variety and canopy level was not significantly different. However, the lowest canopy level recorded the lowest value for g_s. The g_s values were also fluctuating among the stages observed.

The leaves of laterals with spike recorded significantly higher g_s compared to laterals without spike in both Panniyur 1 and Karimunda.

4.5.8 Sub-stomatal CO_2 concentration (Ci)

The internal CO_2 level recorded by the leaves were significantly higher in Karimunda (263.14 μmol mol^{-1}) compared to Panniyur 1 (247.66 μmol mol^{-1}) (table 28 and fig. 24a-b). The variety x canopy interaction did not differ significantly for Ci . The Ci recorded at the various stages was significantly different between the varieties. The influence of different stages on Ci was different for the varieties as the fluctuation trend was varying between the varieties. However, in both the varieties, the Ci levels showed a decreasing trend towards berry maturity. The Ci recorded by the laterals with spikes was significantly higher (262.41 μmol mol^{-1}) as compared to laterals without spikes (247.10 μmol mol^{-1}).

4.6 Biochemical parameters

4.6.1 Chlorophyll content

The chlorophyll content of leaves was analysed at weekly interval starting from opening to the full growth of leaf (table 29 and fig. 25a).

Chlorophyll content of leaves differed significantly among stages in both the varieties. Chlorophyll 'a' content in Panniyur 1 was either on par or higher than Karimunda during all the stages observed from unfurling to 35 days after opening of leaves. Chlorophyll 'b' and total chlorophyll also exhibited similar trend. Chlorophyll 'a' content increased gradually from day one till the leaf

Table 27. Stomatal conductance (mol $m^{-2} s^{-1}$) of the leaves at various developmental stages of the laterals in black pepper

Stages	Canopy								Lateral					
	Lower		Middle		Upper		Average		With out spike		With spike		Average	
	KM	P1	KM	P1	KM	P1	KM	P1	KM	P1	KM	P1	without spike	with spike
Flushing & flowering	0.077	0.137	0.139	0.234	0.142	0.262	**0.119**	**0.211**	0.069	0.154	0.170	0.268	**0.111**	**0.219**
Spike development	0.117	0.140	0.108	0.181	0.134	0.178	**0.119**	**0.166**	0.094	0.114	0.145	0.219	**0.104**	**0.182**
Berry set	0.121	0.202	0.167	0.198	0.156	0.190	**0.148**	**0.197**	0.100	0.130	0.195	0.263	**0.115**	**0.229**
Early berry development	0.137	0.102	0.229	0.128	0.186	0.107	**0.184**	**0.112**	0.145	0.066	0.223	0.159	**0.105**	**0.191**
Late berry development	0.058	0.056	0.056	0.055	0.095	0.051	**0.070**	**0.054**	0.048	0.039	0.091	0.069	**0.044**	**0.080**
Berry maturity	0.123	0.070	0.134	0.111	0.099	0.086	**0.118**	**0.089**	0.121	0.057	0.116	0.121	**0.089**	**0.118**
Harvest	0.081	0.091	0.056	0.080	0.077	0.069	**0.071**	**0.080**	0.074	0.074	0.069	0.086	**0.074**	**0.078**
CD	NS						** 0.034		NS				** 0.034	
Average	**0.102**	**0.114**	**0.127**	**0.141**	**0.127**	**0.135**	**0.118**	**0.130**	**0.093**	**0.091**	**0.144**	**0.169**	**0.092**	**0.157**
CD	NS						* 0.009		* 0.012				** 0.011	

Table 28. Sub-stomatal CO_2 (µmol mol^{-1}) concentration in the leaves at various developmental stages of the laterals in black pepper

Stages	Canopy								Lateral					
	Lower		Middle		Upper		Average		Without spike		With spike		Average	
	KM	P1	KM	P1	KM	P1	KM	P1	KM	P1	KM	P1	Without spike	With spike
Flushing & flowering	269.55	252.98	274.03	260.48	276.29	268.57	**273.29**	**260.68**	263.03	254.42	283.55	266.94	**258.73**	**275.24**
Spike development	279.41	248.05	275.35	235.79	275.10	247.37	**276.62**	**243.73**	266.13	223.89	287.11	263.58	**245.02**	**275.35**
Berry set	277.06	257.82	258.75	266.25	274.77	261.62	**270.19**	**261.90**	262.35	247.10	278.04	276.69	**245.72**	**277.37**
Early berry development	248.17	268.09	264.23	272.78	265.87	260.09	**259.42**	**266.99**	252.09	263.74	266.76	270.23	**257.91**	**268.49**
Late berry development	240.92	224.37	236.30	236.13	264.56	234.44	**247.26**	**233.00**	244.48	222.05	250.04	234.16	**233.66**	**246.60**
Berry maturity	247.74	243.67	240.68	233.62	265.83	223.77	**248.42**	**234.52**	249.88	233.37	246.95	235.68	**241.62**	**241.31**
Harvest	262.37	228.51	270.57	268.57	267.30	236.32	**266.75**	**232.82**	264.50	229.60	268.99	236.04	**247.05**	**252.51**
CD	** 18.48						** 10.67		NS				** 10.67	
Average	**260.75**	**246.21**	**259.99**	**253.37**	**269.96**	**247.45**	**263.14**	**247.66**	**257.49**	**239.17**	**268.78**	**254.76**	**247.10**	**262.41**
CD	NS						** 3.56		NS				** 3.56	

Gas exchange parameters at various stages of development in black pepper

Fig. 23a Variation in stomatal conductance (g_s) between varieties

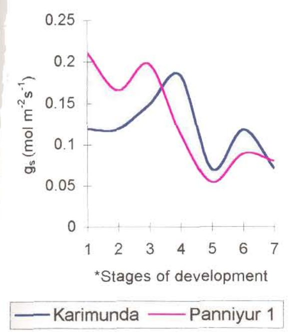


Fig. 23b Variation in g_s between the type of laterals

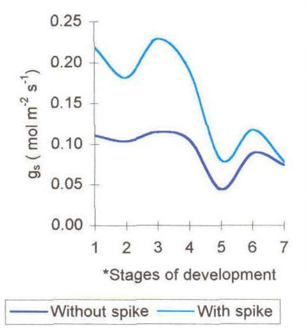


Fig. 24a Variation in sub-stomatal CO_2 concentration between varieties

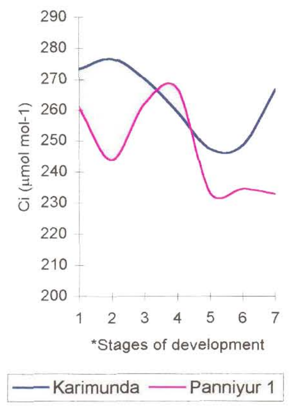
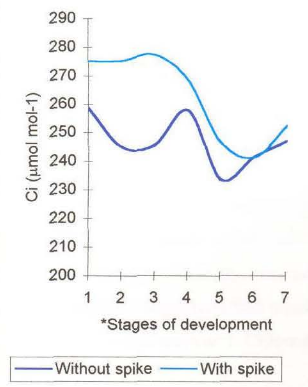


Fig. 24b Variation in Ci between the type of laterals



*1.Flushing and flowering 2. Spike development 3. Berry set 4. Early berry development 5. Late berry development 6. Berry maturity 7. Harvest attained its full growth in size. Even though Chlorophyll 'b' and total chlorophyll differed significantly among stages in the varieties no significant difference was observed in these two parameters between Karimunda and Panniyur 1, on the 35th day. Panniyur 1 recorded significantly higher chlorophyll 'b' and total chlorophyll during all the stages compared to Karimunda except on 35th day. Chlorophyll 'a' was higher in Karimunda (0.674 mg g^{-1}) compared to Panniyur 1(0.633 mg g^{-1}) whereas total chlorophyll was higher in Panniyur 1 (1.728 mg g^{-1}) compared to Karimunda (1.685 mg g^{-1}) on the 35th day. In all the corresponding stages, chlorophyll 'b' content was higher in both Karimunda and Panniyur 1 compared to chlorophyll 'a'.

The chlorophyll 'a','b' and total content of leaves at different stages of development of the laterals are presented in table 30 a to c and fig. 25b. The chlorophyll 'a' content differed significantly between varieties, canopy levels, laterals and stages. The average chlorophyll 'a' content was higher in Karimunda (0.605 mg g^{-1}) compared to Panniyur 1 (0.595 mg g^{-1}). Among the canopy levels, middle canopy recorded higher Chlorophyll 'a' content compared to lower and upper canopies in both Karimunda and Panniyur 1.

The chlorophyll 'a' content varied significantly among stages and it was the highest during berry development in both Panniyur 1 and Karimunda. There was no definite pattern of accumulation of chlorophyll 'a' during the various developmental stages of the lateral. The varietal response also was different during the various stages.

The laterals also differed significantly at five per cent level for the chlorophyll 'a' content. Spike bearing laterals recorded more chlorophyll 'a' compared to laterals without spike, in both Karimunda and Panniyur 1 during all the stages.

Chlorophyll 'b' content of leaves did not differ significantly between varieties. However, the stages and the interaction between variety and canopy differed significantly. Anyway, there was no definite trend in chlorophyll 'b' content of leaves between the stages. The middle canopy recorded significantly higher chlorophyll 'b' content in both Karimunda and Panniyur 1. Chlorophyll 'b'

Table 29. Chlorophyll content (mg g^{-1}) during leaf area development in black pepper

Days after flushing	**Chlorophyll a**		**Chlorophyll b**		**Total chlorohyll**	
	KM	**P1**	**KM**	**P1**	**KM**	**P1**
1	0.066	0.066	0.093	0.100	0.159	0.165
7	0.120	0.172	0.188	0.281	0.307	0.452
14	0.223	0.361	0.371	0.615	0.593	0.974
21	0.458	0.525	0.607	0.829	1.063	1.351
27	0.596	0.613	0.843	1.046	1.436	1.654
35	0.674	0.633	1.106	1.100	1.685	1.728
CD	**** 0.059**		**** 0.111**		**** 0.168**	

Table 30a. Chlorophyll 'a' (mg g^{-1}) content of leaves at various developmental stages of the lateral in black pepper

stages	Canopy								Lateral					
	Lower		Middle		Upper		Average		without spike		with spike		Average	
	KM	P1	KM	P1	KM	P1	KM	P1	KM	P1	KM	P1	Without Spike	With Spike
Flushing and flowering	0.539	0.454	0.725	0.576	0.539	0.468	**0.601**	**0.499**	0.572	0.465	0.630	0.534	**0.518**	**0.582**
Spike development	0.559	0.622	0.665	0.715	0.528	0.607	**0.584**	**0.648**	0.574	0.633	0.594	0.663	**0.603**	**0.629**
Berry set	0.563	0.565	0.711	0.691	0.537	0.520	**0.604**	**0.599**	0.599	0.574	0.609	0.610	**0.586**	**0.610**
Berry development	0.639	0.667	0.792	0.741	0.603	0.628	**0.678**	**0.679**	0.668	0.666	0.688	0.692	**0.667**	**0.690**
Berry maturity	0.596	0.578	0.734	0.687	0.573	0.565	**0.634**	**0.610**	0.612	0.561	0.655	0.658	**0.587**	**0.657**
Harvest	0.507	0.505	0.612	0.606	0.470	0.520	**0.530**	**0.544**	0.510	0.535	0.549	0.552	**0.523**	**0.551**
CD	NS						** 0.027		NS				** 0.027	
Average	**0.567**	**0.565**	**0.706**	**0.669**	**0.542**	**0.552**	**0.605**	**0.595**	**0.589**	**0.572**	**0.621**	**0.618**	**0.581**	**0.620**
CD	** 0.019						* 0.008		NS				* 0.011	

Table 30 b. Chlorophyll 'b' (mg g^{-1}) content of leaves at various developmental stages of the lateral in black pepper

stages	Canopy								Lateral					
	Lower		Middle		Upper		Average		Without spike		With spike		Average	
	KM	P1	KM	P1	KM	P1	KM	P1	KM	P1	KM	P1	Without spike	With Spike
Flushing and flowering	0.802	0.659	1.120	0.875	0.797	0.709	0.906	0.748	**0.838**	**0.699**	0.975	0.797	**0.768**	**0.886**
Spike elongation	0.851	0.961	1.019	1.118	0.778	0.921	0.883	1.000	**0.851**	**0.981**	0.914	1.019	**0.916**	**0.967**
Berry set	0.840	0.868	1.121	1.091	0.816	0.792	0.926	0.917	**0.898**	**0.889**	0.954	0.945	**0.893**	**0.950**
Berry development	1.019	1.072	1.255	1.165	0.977	1.020	1.084	1.085	**1.041**	**1.059**	1.126	1.112	**1.050**	**1.119**
Berry maturity	0.966	0.893	1.181	1.087	0.893	0.877	1.013	0.952	**0.963**	**0.872**	1.063	1.033	**0.918**	**1.048**
Harvest	0.776	0.769	0.927	0.963	0.705	0.778	0.803	0.837	**0.788**	**0.816**	0.818	0.857	**0.802**	**0.837**
CD	NS						* * 0.040		NS				* * 0.040	
Average	**0.876**	**0.870**	**1.104**	**1.050**	**0.828**	**0.849**	**0.936**	**0.923**	**0.896**	**0.886**	**0.975**	**0.960**	**0.891**	**0.968**
CD	* * 0.028						NS		NS				* * 0.016	

Table 30 c. Total chlorophyll (mg g^{-1}) content of leaves at various developmental stages of the lateral in black pepper

Stages	Canopy								Lateral					
	Lower		Middle		upper		Average		Without spike		With spike		Average	
	KM	P1	KM	P1	KM	P1	KM	P1	KM	P1	KM	P1	Without Spike	With Spike
Flushing and flowering	1.337	1.110	1.840	1.447	1.333	1.175	**1.504**	**1.244**	1.406	1.161	1.601	1.327	**1.284**	**1.464**
Spike elongation	1.407	1.579	1.680	1.828	1.303	1.525	**1.463**	**1.644**	1.421	1.610	1.505	1.678	**1.516**	**1.591**
Berry set	1.400	1.430	1.828	1.778	1.350	1.309	**1.526**	**1.506**	1.493	1.459	1.559	1.552	**1.476**	**1.555**
Berry development	1.654	1.734	2.042	1.902	1.576	1.644	**1.757**	**1.760**	1.705	1.720	1.809	1.800	**1.713**	**1.805**
Berry maturity	1.558	1.468	1.910	1.770	1.462	1.438	**1.643**	**1.559**	1.572	1.430	1.715	1.687	**1.501**	**1.701**
Harvest	1.280	1.272	1.535	1.566	1.172	1.295	**1.329**	**1.377**	1.295	1.348	1.363	1.406	**1.322**	**1.385**
CD	** 0.107						** 0.062		NS				** 0.062	
Average	**1.439**	**1.432**	**1.806**	**1.715**	**1.366**	**1.398**	**1.537**	**1.515**	**1.482**	**1.455**	**1.592**	**1.575**	**1.468**	**1.584**
CD	* * 0.044						* 0.019		NS				** 0.025	

Biochemical characters at various stages of development of the lateral in black pepper

Fig. 25a Leaf chlorophyll development in black pepper

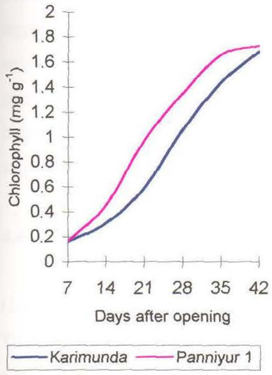


Fig. 25b Variation in chlorophyll content of leaves between varieties

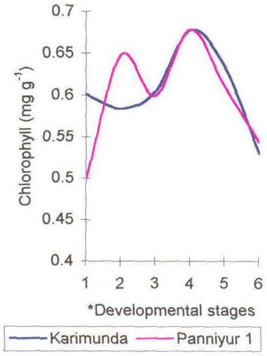


Fig. 26a Variation in carbohydrate content of leaves between varieties

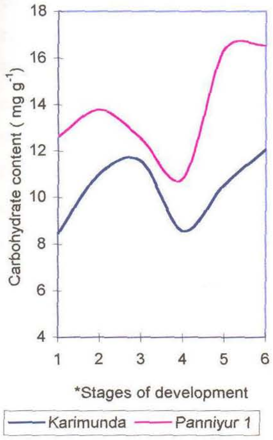
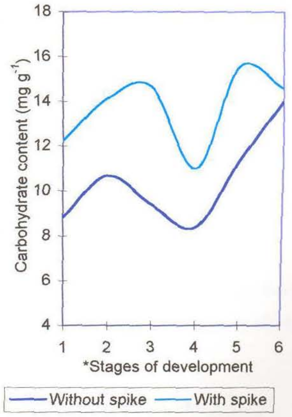


Fig. 26b Variation in cabohydrate content between laterals



*1.Flushing and flowering 2. Spike development 3. Berry set 4. berry development 5. Berry maturity 6. Harvest content was the maximum during berry development stage in both the varieties. The leaves from spike bearing laterals recorded significantly higher chlorophyll 'b' content compared to laterals without spike.

The total chlorophyll content of leaves also differed significantly between varieties. The middle canopy level had significantly higher total chlorophyll content compared to lower and upper canopies. The stages also differed significantly for total chlorophyll content. Maximum chlorophyll content was recorded during the berry development stage. The laterals also differed significantly for total chlorophyll content. The spike bearing laterals recorded a higher total chlorophyll content compared to laterals without spikes during all the stages observed.

4.6.2 Carbohydrate content

The carbohydrate content of leaves was significantly higher in Panniyur 1 (13.71 mg g^{-1}) compared to Karimunda (10.37 mg g^{-1}) (Table 31and fig. 26a -b). The interaction between variety and canopy level also differed significantly in the accumulation of carbohydrates in the leaves in both the varieties. While the accumulation of carbohydrate was on par in all the canopy levels in Karimunda, this was significantly higher in the lower canopy in Panniyur 1. The carbohydrate content also varied significantly among stages in both the varieties. The carbohydrate content was significantly higher in Panniyur 1 compared to Karimunda during all the stages observed. The trend in the accumulation of carbohydrate in the leaves was similar for both Panniyur 1 and Karimunda for all the stages observed. Total carbohydrate content increased from flushing and flowering to berry set and then the content was decreased during berry development stage. It again showed an increasing trend towards berry maturity and harvest stage. The maximum content of carbohydrate of leaves was recorded during the harvest stage of spikes in the lateral in both the varieties.

In both the varieties, the spike bearing laterals recorded significantly high content of carbohydrates compared to laterals without spikes in all the stages observed.

Table 31. Carbohydrate content (mg g^{-1}) of leaves at various developmental stages of the laterals in black pepper

stages	Canopy								Lateral					
	Lower		middle		upper		Average		Without spike		With spike		Average	
	KM	P1	KM	P1	KM	P1	KM	P1	KM	P1	KM	P1	Without spike	With spike
Flushing and flowering	6.76	14.46	9.01	12.34	9.62	11.05	**8.46**	**12.62**	7.04	10.61	9.88	14.63	**8.82**	**12.25**
Spike elongation	10.21	14.96	11.13	12.96	11.73	13.42	**11.03**	**13.78**	9.87	11.48	12.18	16.07	**10.68**	**14.13**
Berry set	10.29	13.88	12.72	11.76	11.66	11.95	**11.56**	**12.53**	8.81	9.97	14.29	15.09	**9.39**	**14.69**
Berry development	7.97	10.30	8.65	10.76	9.07	11.39	**8.56**	**10.82**	7.55	9.21	9.57	12.43	**8.38**	**10.99**
Berry maturity	11.30	19.28	9.30	14.27	11.07	15.55	**10.55**	**16.36**	8.67	14.04	12.43	18.69	**11.36**	**15.56**
Harvest	12.06	17.26	12.78	15.17	11.34	17.21	**12.06**	**16.54**	11.63	16.37	12.50	16.72	**14.00**	**14.61**
CD	NS						** 1.534		NS				** 1.534	
Average	**9.76**	**15.02**	**10.60**	**12.88**	**10.75**	**13.43**	**10.37**	**13.71**	**8.93**	**11.84**	**11.81**	**15.60**	**10.44**	**13.71**
CD	** 1.084						** 0.626		NS				**0.626	

Table 32.Total phenol content (mg g^{-1}) of leaves at various developmental stages of the lateral in black pepper

stages	Canopy								Lateral					
	Lower		middle		upper		Average		Without spike		With spike		Average	
	KM	P1	KM	P1	KM	P1	KM	P1	KM	P1	KM	P1	Without spike	With spike
Flushing and flowering	1.186	1.117	1.260	1.267	1.230	1.247	**1.225**	**1.210**	1.184	1.116	1.267	1.304	**1.150**	**1.286**
Spike elongation	1.047	1.130	1.104	1.340	1.283	1.413	**1.145**	**1.294**	1.013	1.127	1.276	1.462	**1.070**	**1.369**
Berry set	1.197	1.127	1.173	1.183	1.267	1.327	**1.212**	**1.212**	1.091	1.091	1.333	1.333	**1.091**	**1.330**
Berry development	1.213	1.110	1.355	1.310	1.457	1.477	**1.342**	**1.299**	1.272	1.209	1.411	1.389	**1.241**	**1.400**
Berry maturity	1.944	1.740	2.083	1.873	2.250	2.014	**2.092**	**1.876**	1.934	1.776	2.251	1.976	**1.855**	**2.113**
Harvest	2.297	1.640	2.340	1.847	2.453	1.863	**2.363**	**1.783**	2.271	1.747	2.456	1.820	**2.009**	**2.138**
CD	NS						** 0.122		NS				** 0.122	
Average	**1.480**	**1.311**	**1.553**	**1.470**	**1.657**	**1.557**	**1.563**	**1.446**	**1.461**	**1.344**	**1.666**	**1.547**	**1.402**	**1.607**
CD	* * 0.086						** 0.050		NS				** 0.050	

4.6.3 Phenol content

The phenolics of leaves at the various stages of development was analysed and presented in table 32 and fig. 27a-b. The average phenol content of leaves was found to be significantly higher in Karimunda (1.563 mg g^{-1}) compared to Panniyur 1 (1.446 mg g^{-1}). This was true irrespective of canopy, stages or the type of lateral. The canopy levels were significantly different for the phenol content of leaves in both Karimunda and Panniyur 1. The phenol content was significantly higher in the leaves from the top most canopy in both the varieties. The phenol content also differed significantly among stages. This was higher during berry maturity and harvesting stages of spikes in the laterals. The other stages such as flushing and flowering, spike development and berry set were on par between the varieties. The leaves from the laterals with spikes had significantly high phenol content compared to those without spikes. This was also true during all the stages observed especially during berry maturity and harvest stage in the lateral.

4.6.4 Amino acid content

There was no varietal variation with respect to the amino acid content of leaves (table 33 and fig. 28a-b). However, the interaction between variety and canopy was significantly different. The amino acid content of leaves also differed significantly among canopy levels in Karimunda. The middle and top canopy levels were on par but had significantly higher amino acid compared to the lower canopy level in Karimunda. However, in Panniyur 1, the canopy levels were on par.

Amino acid content of leaves differed significantly among stages in both Karimunda and Panniyur 1. This was the highest during flushing and flowering and spike development in both Karimunda and Panniyur 1. However, the amino acid content of leaves during the different stages was on par between Panniyur 1 and Karimunda except at spike development stage.

The spike bearing laterals had significantly higher content of amino acid (0.294 mg g^{-1}) compared to laterals without spikes (0.211 mg g^{-1}) during all the stages.

Table 33. Amino acid content (mg g^{-1}) of leaves at various developmental stages in black pepper

Stages	Canopy								Lateral					
	Lower		Middle		Upper		Average		Without spike		With spike		Average	
	KM	P1	KM	P1	KM	P1	KM	P1	KM	P1	KM	P1	Without spike	With spike
Flushing and flowering	0.271	0.323	0.340	0.291	0.327	0.317	**0.313**	**0.310**	0.269	0.214	0.356	0.407	**0.241**	**0.382**
Spike elongation	0.263	0.257	0.313	0.265	0.327	0.290	**0.301**	**0.270**	0.259	0.217	0.343	0.324	**0.238**	**0.334**
Berry set	0.224	0.258	0.252	0.269	0.288	0.272	**0.255**	**0.266**	0.208	0.209	0.302	0.323	**0.208**	**0.312**
Berry development	0.218	0.272	0.349	0.335	0.300	0.278	**0.289**	**0.295**	0.230	0.233	0.348	0.357	**0.232**	**0.353**
Berry maturity	0.173	0.173	0.193	0.180	0.198	0.185	**0.188**	**0.180**	0.178	0.170	0.199	0.189	**0.174**	**0.194**
Harvest	0.167	0.162	0.194	0.179	0.206	0.179	**0.189**	**0.173**	0.177	0.167	0.201	0.179	**0.172**	**0.190**
CD	NS						** 0.029		NS				**0.027	
Average	**0.219**	**0.241**	**0.274**	**0.253**	**0.274**	**0.253**	**0.256**	**0.249**	**0.220**	**0.202**	**0.291**	**0.297**	**0.211**	**0.294**
CD	** 0.019						NS		** 0.016				** 0.017	

Table 34. Rf value and intensity of protein bands in black pepper varieties

Variety	Bands						
	1	2	3	4	6	7	8
	Rf value						
	0.35	0.40	0.47	0.55	0.64	0.7	0.76
Karimunda	* *	* *	Nil	* * *	Nil	*	* * *
Panniyur 1	* * *	* *	* *	* * * *	* * *	* *	* * * *

* * * * Major	* * * Intermediate	* * Minor	* Traces

Biochemical characters at various stages of development of the lateral in black pepper

Fig. 27a Variation in total phenol content of leaves between varieties

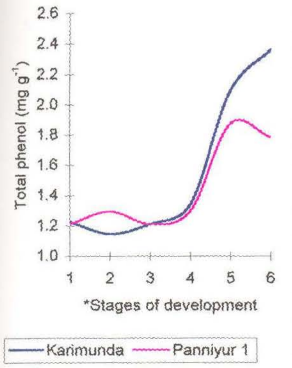


Fig. 27b Variation in phenol content between the type of laterals

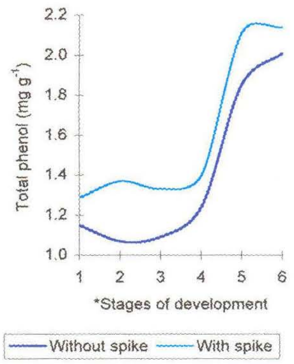


Fig. 28a Variation in aminoacid content between varieties

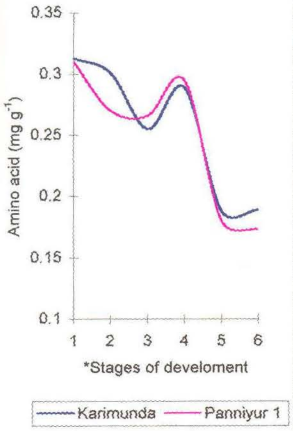
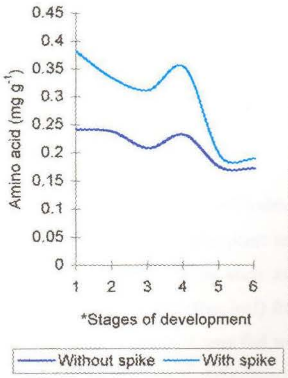


Fig. 28b Variation in aminoacid content between laterals



*1.Flushing and flowering 2. Spike development 3. Berry set 4. berry development 5. Berry maturity 6. Harvest

4.6.5 Electrophoretic pattern of berry proteins

The electrophoretic pattern of berry proteins in the laterals of Karimunda and Panniyur 1 are presented in table 34 and have been outlined in the form of zymogram (fig. 29).

During berry set and berry development, the samples could not yield a homogenate with enough protein for electrophoretic analysis. However, this was successful during berry maturity stage.

The results showed variation in the electrophoretic pattern between genotypes. In Karimunda, altogether six bands were seen whereas in Panniyur 1, eight bands were seen and the R_f values ranged from 0.35 to 0.76. The banding pattern among the replication within a variety was repeatable and the zymogram did not show intra-varietal differences in Panniyur 1. However, banding pattern of replications in Karimunda varied showing intra-varietal variability.

In variety Panniyur 1, bands were designated as 1 to 8. Three major bands (band no. 4, 5 and 8) with deep staining could be identified. Two bands were intermediate in staining (band no. 1 and 6), while others (band no. 2, 3 and 7) were minor, as judged by staining intensities.

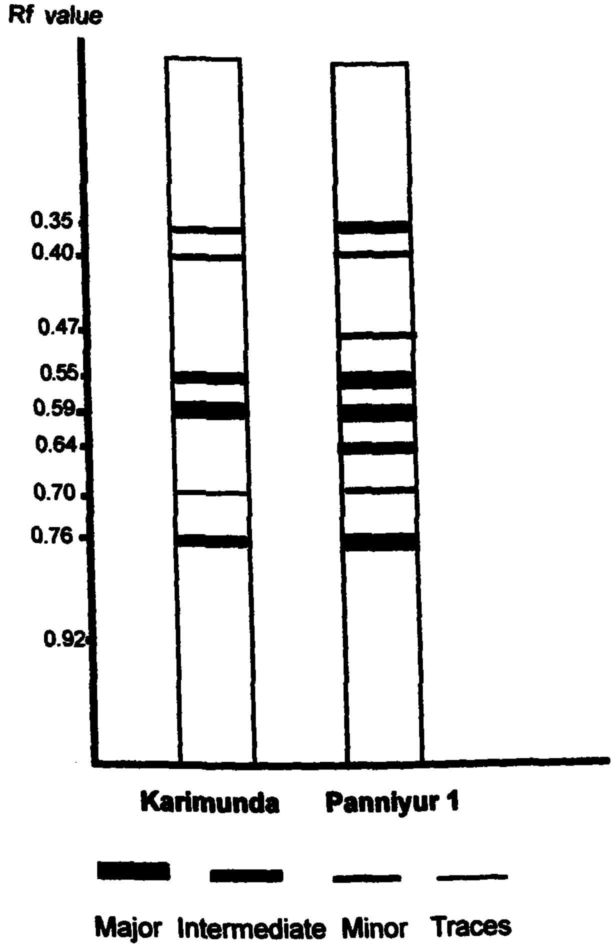
In Karimunda, only six bands could be seen. The bands designated as 3 and 6 in Panniyur 1, were absent in this variety. On the basis of intensity of staining, one major band (band no. 5) could be identified. Two bands (band no. 4 and 8) were intermediate in staining intensities while the other bands (band no. 1 and 2) were minor components. Band 7 was very feeble.

The bands varied considerably with respect to their staining intensities between the varieties. The staining intensity was more in the variety Panniyur 1 for all the bands except band no. 2 and 5.

4.7 Studies on assimilate partitioning using labelled photosynthates

The experiment was conducted in potted bush pepper plant using intact leaves at four different developmental stages of the laterals such as flushing, flowering, berry set and berry development. A single leaf (flag leaf) from potted bush pepper plants of varieties Karimunda and Panniyur 1 was fed with $^{14}CO_2$

Fig. 29 Electrophoretic pattern of berry proteins in black pepper varieties.



and the sink effect of the different organs of the plant was investigated at the four developmental stages mentioned. The retention of radioactivity was measured in various parts of the plant and the radioactive counts and partitioning were tabulated and presented in table 35 a-c.

The result indicated variation in the pattern of partitioning of photosynthetic assimilates during different developmental phases of the lateral (fig. 30a-h and fig. 31a-d). In Karimunda, 97.42 per cent of the activity could be traced from the fed leaf itself within 24 hours, at flushing stage. The stem portion of the lateral retained only 1.6 per cent of the activity. The total activity retained in the lateral was 99.03 per cent leaving practically no significant activity in other parts of the plant.

In the variety Panniyur 1 also, the fed leaf retained significantly higher percentage of activity (89.24) during flushing stage. The activity retained in the stem of the lateral was 9.28 per cent, which was higher compared to the variety Karimunda. The other aerial parts of the plant and the root portion retained only 0.27 per cent and 1.20 per cent of activity respectively, after 24 hours of feeding.

At flowering stage also, the activity retained in the source leaf was highest (89.11%) compared to other organs in Karimunda. Out of the total $^{14}CO_2$ partitioned, developing spikes shared 9.33 per cent of the activity. The stem of the laterals had 1.0 per cent activity and the other aerial parts and root received less than 1.0 per cent of the activity.

In Panniyur 1, during flowering stage, only 39.80 per cent of activity remained in the fed leaf, while the activity translocated to the spike was as high as 57.53 per cent. However, the stem of the lateral retained only 2.31 per cent and the other aerial parts of the plant and the roots retained only 2.68 and 0.08 per cent respectively.

At berry set stage, the fed leaf retained 72.48 per cent of the activity while 10.22 per cent was translocated to the spike, 8.65 per cent to the stem of the lateral, 8.24 per cent to the other aerial parts and 0.4 per cent to the roots in Karimunda. In Panniyur 1, at this stage, the spike received the maximum (80.23%) of the total radioactivity fixed by the plant. Only 16.13 per cent of the

Table 35 a. Translocation and partitioning of labelled photosynthates (cpm g^{-1}) in bush pepper

Stages	Part sampled											
	Leaf		Spike		Stem		Other parts		Root		Total	
	KM	P1	KM	P1	KM	P1	KM	P1	KM	P1	KM	P1
Flushing	44624.7	149179.1	0.0	0.0	738.8	15512.9	226.4	448.3	215.4	2012.7	45805.3	167153.0
Flowering	114168.6	162053.7	11963.0	234256.8	1255.7	9406.0	401.0	1093.6	337.4	340.0	128125.7	407150.1
Berryset	125540.4	44785.6	17700.8	222736.0	14985.9	664.0	14277.0	9115.2	700.5	301.9	173204.6	277602.7
Berry development	10423.5	21232.3	26486.0	61968.2	44031.7	216.8	896.4	1421.6	126.2	192.4	81963.8	85031.3
CD	NS		NS		NS		NS		NS		NS	

Table 35 b. Percentage partitioning of labelled photosynthates in bush pepper

Stages	Part sampled									
	Leaf		Spike		Stem		Other parts		Root	
	KM	P1	KM	P1	KM	P1	KM	P1	KM	P1
Flushing	97.42	89.24	0.00	0.00	1.61	9.28	0.51	0.27	0.50	1.20
Flowering	89.11	39.80	9.33	57.53	1.00	2.31	0.31	2.68	0.26	0.08
Berry set	72.48	16.13	10.22	80.23	8.65	0.24	8.24	3.28	0.40	0.11
Berry development	12.72	24.97	32.32	72.88	53.72	0.25	1.10	1.67	0.15	0.22

Partitioning of labelled photosynthates at various stages of development in bush pepper

Fig. 30a partitioning during flushing stage in Karimunda

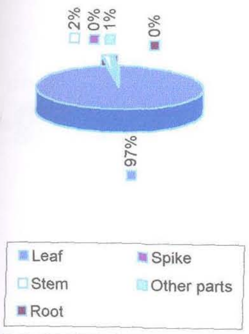


Fig. 30b Partitioning during flushing stage in Panniyur 1

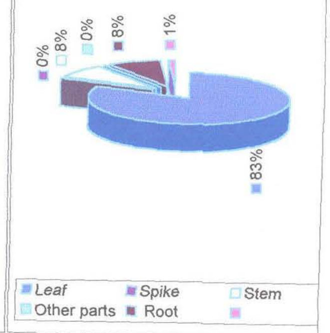


Fig. 30c Partitioning during flowering stage in Karimunda

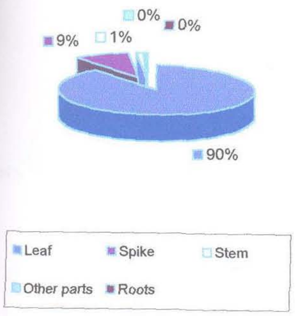
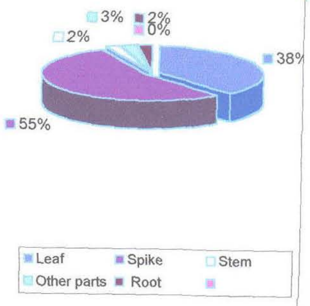


Fig. 30d Partitioning during flowering stage in Panniyur1



Partitioning of labelled photosynthates at various stages of development in bush pepper

Fig. 30e Partitioning during berry set stage in Karimunda

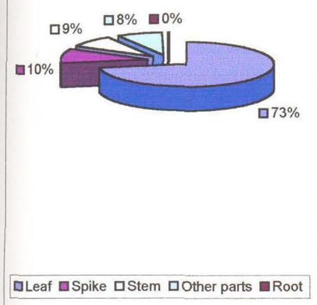


***Fig. 30f Partitioning during* berryset stage in Panniyur 1**

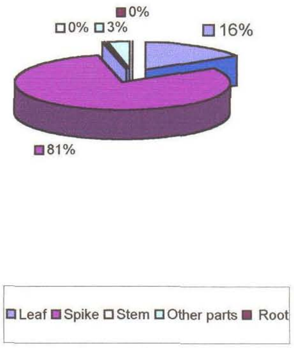


Fig. 30g Partitioning during berry development stage in Karimunda

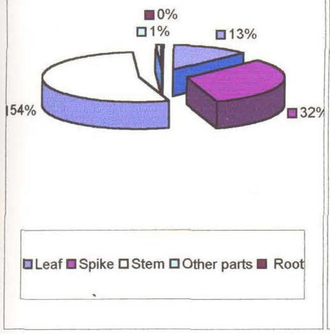
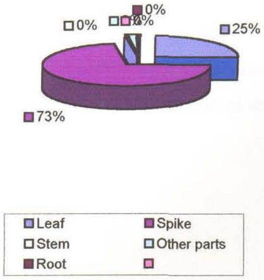


Fig. 30h Partitioning during berry development stage in Panniyur 1



activity was retained by the fed leaf while the radio activity effluxed out from the fed leaf to the other organs such as stem of the lateral (0.24 %) other aerial parts (3.28 %) and root (0.11 %) were low.

At berry development stage, the stem of the lateral in Karimunda retained the maximum radioactivity (53.72 %). Out of the partitioned $^{14}CO_2$, the fed leaf retained only 12.72 per cent. The spike subtending the fed leaf recorded an activity of 32.32 per cent while translocation to other aerial parts and root was 1.10 per cent.

However, in the variety Panniyur 1, maximum labelled CO_2 was partitioned to the spikes (72.88%) while the activity retained in the fed leaf was only 24.97 per cent. Only 0.25 per cent of the total $^{14}CO_2$ was translocated to the stem of the laterals during berry development stage. The other aerial parts and the roots received only 1.67 per cent and 0.22 per cent of the activity respectively.

The subtending spikes were sampled at different periods after feeding the leaf with $^{14}CO_2$ at berry set and berry development stages (table 35c and fig. 32a-b).

During berry set stage, the translocation of labelled photosynthates from the fed leaf to the spikes increased from the time of feeding till the 3rd day in Karimunda. There after this showed a decline on 5th and 7th day, indicating a dilution effect due to dry matter accumulation. In Panniyur 1, the translocation of labelled photosynthates from fed leaves to the subtending spike continued till one day after feeding. Maximum activity in the spike was traced 24 hrs after feeding and thereafter the activity showed a declining trend during 3rd, 5th and 7th day.

At berry development stage, the translocation of labelled photosynthates from fed leaves to the spikes was the maximum on the 3rd day after feeding in both Karimunda and Panniyur 1. Thereafter the activity declined on the 5th and 7th day.

Partitioning of labelled photosynthates by the component organs during *various stages of development in bush pepper*

Fig. 31a Partitioning by leaves

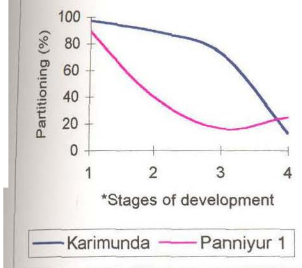


Fig. 31b Partitioning by spikes

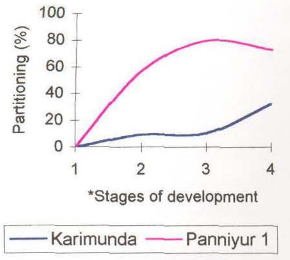


Fig. 31c Partitioning by stem

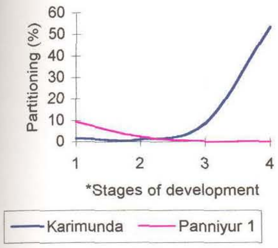
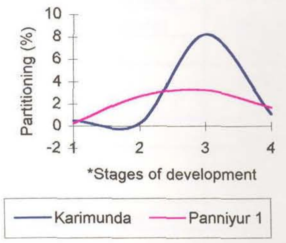


Fig. 31d Partitioning by other aerial parts



*** 1. Flushing 2. Flowering 3. Berry set 4. Berry development**

Fig. 32a Fixing of labelled photosynthates at different *periods after feeding during* berry set

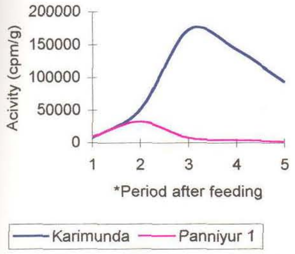
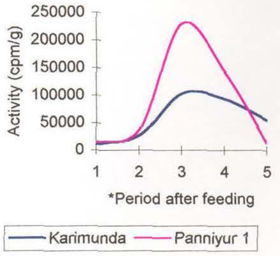


Fig. 32b Fixing of labelled photosynthates at diffent *periods after feeding during* berry development



*1. **2hrs** 2. **24 hrs** 3. **3days** 4. **5days** 5. **7days**

Table 35c. Partitioning of labelled photosynthates (cpm) at different periods after feeding in bush pepper during berry set and berry development

Period of sampling	Berry set		Berry development	
	KM	P1	KM	P1
2 hrs	7681.5	9406.2	11326.7	14334.6
24 hrs	51938.3	33046.0	26486.1	37180.9
3 days	173433.3	7843.3	102990.4	229979.5
5 days	142384.5	4644.5	93629.8	143325.0
7 days	93457.2	1672.2	54738.1	13629.4
CD	NS		NS	

Table 36. Correlation between morphological characters and dry pepper yield

Sl. No	Morphological characters	Correlation coefficient
A	Character of the lateral	
1	Number of leaves	0.002
2	Leaf area	0.123
3	Length of lateral	0.092
4	Number of nodes	-0.044
5	Fresh weight of stem	0.267 **
6	Fresh weight of leaf	0.255**
7	Total fresh weight of lateral	0.426**
8	Dry weight of stem	0.177 *
9	Dry weight of leaf	0.166
10	Total dry weight of lateral	0.445 **
B	Spike and berry characters	
13	Spike length	0.439**
14	Average spike weight	0.382**
15	Number of developed berries	0.474**
16	Number of undeveloped berries	0.017
17	Total number of berries per spike	0.457**
18	Hundred berry weight	0.334 **
19	Hundred berry volume	0.298**
C	Yield characters of the plant	
20	Dry weight percentage of berries	0.339**
21	Number of spikes	0.541**
22	Fresh weight of spikes	0.935**
23	Fresh weight of berries	0.987**
Table value(0.05) 0.174, (0.01) 0.228		

4.8 Correlation studies

Various morphological traits, gas exchange parameters and biochemical characters were correlated with dry pepper yield and inter relationships among them were worked out.

4.8.1 Correlation between morphological characters and yield

Characters of the lateral, spike and berry, and yield characters of the vine were correlated with dry pepper yield and the correlation coefficients are presented in table 36 and fig. 33a-f.

Among the characters of laterals studied, total dry weight of lateral (r = 0.445), total fresh weight of lateral (r = 0.426), fresh weight of stem (r = 0.267) and fresh weight of leaf (r = 0.255) had significant correlation with dry pepper yield. Dry weight of stem also was positively correlated (r = 0.177) with yield at five per cent level. Number of nodes per lateral was negatively correlated with yield. The other characters of the lateral, though positively correlated, were not significant.

Among the spike and berry characters, those showing significant positive correlation with dry pepper yield were number of developed berries (r = 0.474), total number of berries (r = 0.457), length of spike (r = 0.440), hundred berry weight (r = 0.334) and volume (r = 0.298).

Among the yield characters of the plant, total fresh weight of berries (r = 0.987) and fresh weight of spikes (r = 0.935) were highly correlated with yield. Number of spikes in the plant (r = 0.541) and the dry weight percentage of berries (r = 0.339) also had significant association with yield.

The inter correlation of morphological parameters were worked out and presented in appendix II.

Number of leaves in the laterals registered significant negative association with berry fresh weight and volume, fresh and dry weight of spikes, number of developed berries in a spike and total fresh and dry weights of the lateral.

Fig. 33a Correlation between total fresh weight of lateral and yield

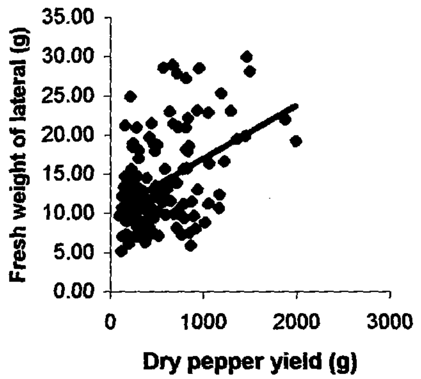


Fig. 33b Correlation between total dry weight of lateral and dry pepper yield

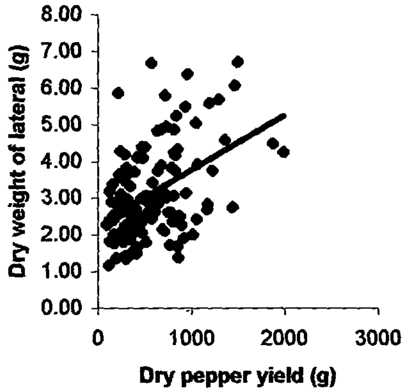


Fig. 33c Correlation between spikelength and dry pepper yield

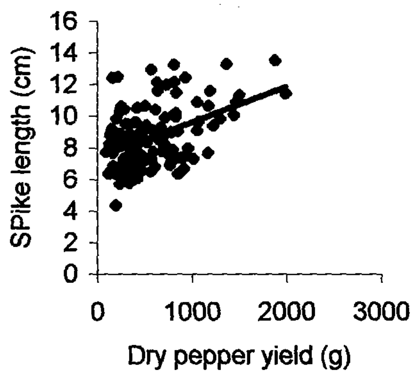


Fig. 33d Correlation between number of developed berries and dry pepper yield

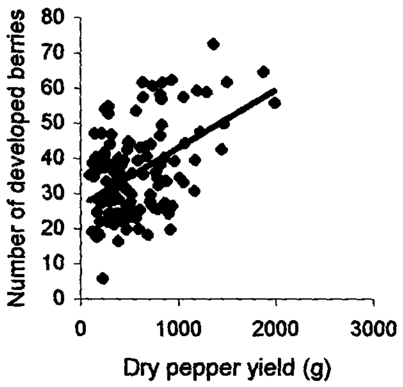


Fig.33e Correlation between fresh spike weight and dry pepper yield

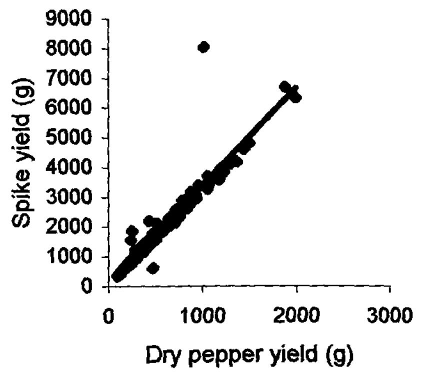
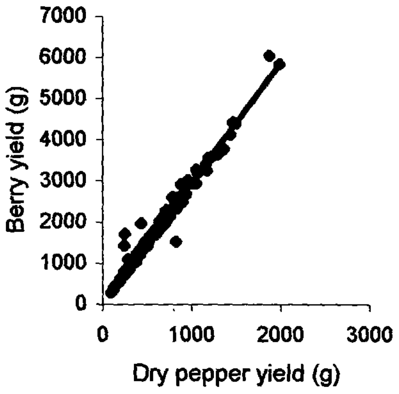


Fig.33f Correlation between fresh weight of berries and dry pepper yield



Leaf area of the lateral showed significant positive correlation with fresh weight and dry weight of spike and stem, leaf dry weight and total dry weight of the lateral.

Weight and volume of hundred berries were significantly correlated with total fresh weight and dry weight of the lateral. However, these characters exhibited negative association with number of nodes and number of spikes in the lateral.

Length of the lateral had significant positive association with fresh weight and dry weight of leaves and number of spikes. However, this character was negatively associated with spike length, average spike weight, berry volume, number of developed berries and total berries in a spike.

Dry weight of the spike was highly correlated with total fresh weight and dry weight of the lateral. Other characters which showed significant correlation with total fresh weight and dry weight of the lateral were spike length, spike fresh weight, weight and volume of berries, number of developed berries and total berries in a spike.

4.8.2 Correlation between gas exchange parameters and yield

The correlation between gas exchange parameters and dry pepper yield was worked out and presented in table 37.

Among the gas exchange parameters, only the photosynthetic rate showed significant positive correlation ($r = 0.195$) with dry pepper yield. Though the parameters such as stomatal conductance, leaf surface temperature and photosynthetically active radiation exhibited positive correlation with yield, their effects were not significant. Stomatal resistance, transpiration rate, vapour pressure deficit and sub-stomatal CO_2 concentration showed negative correlation with yield.

The inter correlation of gas exchange parameters are presented in appendix III. The parameters, which showed significantly high correlation with photosynhtetic rate, were sub-stomatal CO_2 concentration and photosynthetically

Table 37. Correlation between gas exchange parameters and dry pepper yield

Sl. No	Character	Correlation coefficient
1	Photosynthetic rate	0.195 **
2	Stomatal resistance	-0.018
3	Stomatal conductance	0.019
4	Transpiration rate	-0.026
5	Leaf surface temperature	0.026
6	Photosynthetically active radiation	0.050
7	Vapour pressure deficit	-0.048
8	Sub-stomatal CO_2 concentration	-0.001
Table value (0.05) 0.088, (0.01) 0.115		

Table 38. Correlation between biochemical characters and dry pepper yield

Sl. No	Character	Correlation coefficient
1	Chlorophyll 'a'	0.092 *
2	Chlorophyll 'b'	0.112 *
3	Total chlorophyll	0.108 *
4	Carbohydrate	0.089 *
5	Phenolics	0.059
6	Amino acid	0.052
Table value (0.05) 0.088, (0.01) 0.115		

active radiation. Leaf surface temperature registered negative correlation with photosynthetic rate.

Stomatal resistance showed significant negative correlation with transpiration rate, leaf temperature, photosynthetically active radiation and vapour pressure deficit.

Stomatal conductance was negatively correlated with most of the other parameters such as stomatal resistance, transpiration rate, leaf surface temperature, photosynthetically active radiation and vapour pressure deficit.

Transpiration rate showed positive correlation with leaf temperature, photosynthetically active radiation and vapour pressure deficit. However, this parameter had negative association with stomatal conductance and stomatal resistance.

Leaf surface temperature showed positive correlation with vapour pressure deficit and was negatively correlated with sub-stomatal CO_2 concentration.

4.8.3 Correlation between biochemical characters and yield

The correlation between biochemical characters and yield were arrived at and the results are presented in table 38 and the inter correlation matrix is presented in appendix IV.

Among the biochemical characters, chlorophyll 'a' and 'b', total chlorophyll and carbohydrates showed significant positive association with yield. The rest of the parameters such as phenol content and amino acid content though positively correlated were not statistically significant. The correlation coefficients for chlorophyll 'a' and 'b', total chlorophyll and carbohydrate content were 0.093, 0.113, 0.108 and 0.089 respectively.

Chlorophyll 'a', 'b' and total chlorophyll were positively correlated with amino acid content. Phenol content of leaves showed negative correlation with chlorophyll and amino acids.

Discussion

DISCUSSION

The thrust of research in black pepper during the last two decades was mainly on increasing productivity through breeding new varieties and standardising production technology. However, the productivity still remains low. The present investigations on 'Physiological and biochemical aspects of flowering, berry set and development in black pepper (*Piper nigrum* L.)' was aimed at probing the physiological and biochemical basis of productivity in this crop, which is poorly understood. In the present study, attempts were made to analyse morphological, physiological and biochemical parameters associated with growth, development and yield in black pepper. The salient results of the present investigation are briefly discussed hereunder:

5.1 History of experimental plants

Productivity of a crop is the outcome of an integrated set of characters, which are influenced by heredity and environmental factors. It was observed that the annual yield in black pepper was fluctuating over the five years before the commencement of the experiment. The fluctuation was more pronounced in the variety Panniyur 1, compared to Karimunda. Among the five years, the yield recorded by Panniyur 1 was significantly higher during 1993 and 1995 while the yield was on par with Karimunda during 1992, 1994 and 1996, indicating alternate bearing tendencies (fig. 1a). However, the cumulative yield and average yield were significantly higher in Panniyur 1.

Growth characters of the laterals of the previous season are important since the production of laterals during the current season and their growth depends on these characters. It was observed that the number of main laterals, number of leaves per lateral and the total leaf area of the plant prior to the experiment were high in Karimunda. This indicated a longer life span of leaves as well as the retention capacity of the leaf in the variety Karimunda. So this is likely to contribute in photosynthesis and storage of assimilates during off-season.

5.2 Chronological events in the growth and development of laterals

5.2.1 Flushing and flowering

Perennial crops in general bear fruits either on the past season's growth or current season's flushes. Various factors like climate, extension growth and physiological maturity of shoots, previous year's crop load etc. have been reported to influence the phenomenon of flushing, vegetative growth and flower bud differentiation (Evans, 1987).

In black pepper, the first sign of fresh growth in a lateral during a season is indicated by the emergence of leaves from the apical buds known as flushing (plate 5a-b). In the present study, flushing was initiated within a week after the receipt of first rain during the monsoon, during the two years studied. The meteorological data reveal that during the year 1997, the first shower was received on 1st May and a total of 64.2 mm pre-monsoon showers were received by 27th of May. However, the rest of May and the first week of June were devoid of any rainfall and the south-west monsoon commenced only on 8th of June. The first flushing was noticed on 11th June 1997 in Panniyur 1 and six days later in Karimunda. This indicated that the pre-monsoon showers received during May 1997 were insufficient to induce good flushing. During 1998, the first flushing was noticed in Panniyur 1on June 3rd itself and on 9th June in Karimunda. Thus flushing was delayed by 8 days during 1997 season compared to 1998. This may be due to the fact that rainfall received during May 1998 was continuous and higher (124.8 mm) compared to the pre-monsoon showers received during May 1997 (64.2 mm). This also indicates that flushing will be initiated within a week of continuous rainfall. The time of emergence of flushes was six days late in Karimunda compared to Panniyur 1. Thus among the varieties, Panniyur 1 responded to the rains faster and flushed earlier than Karimunda. The initiation of flushing was complete within two weeks in all the observational plants.

Pillai *et al.* (1987) reported that pre-monsoon showers received after a dry spell triggered the flower bud differentiation in pepper. Flushing and flowering could be induced if 70-100 mm rainfall is received or an equivalent quantity of water is provided within a period of about three weeks. The initiation of growth activity in response to the rainfall observed in the present investigation is in conformity with the above findings. Various other researchers also had emphasised the impact of weather parameters on growth and productivity in black pepper (Nalini, 1983 and Rajan, 1985). The mild temperature, heavy rainfall and high relative humidity during the period would be well suited for vegetative growth and probably would have induced and encouraged flushing and flowering in the vines.

In several tropical tree crops, flushing and flowering are often induced by rainfall (Alvim, 1978). Borchert (1983) had shown that flowering in some tropical trees occur in response to decreased water stress, which may be stimulated either by leaf loss or rainfall. These findings also probably explain the response of black pepper to the rainfall.

In the present study, development of spike bearing vegetative flushes in black pepper was limited to an intense period of two months a year, starting from June when the monsoon commences. Majority of the flushes occurred during June-July and the maximum flushing coincided with the periods of heavy monsoon. Period of emergence of growth flushes seems to be slightly extended in Karimunda as sparse flushing is commonly noticed during September when north-east monsoon is received, which is absent in Panniyur 1. Similar observations were made in black pepper by Rajan (1985). In Karimunda, during the same period of crop cycle, actively growing spikes and berries and new flushes are found on individual vines.

It was observed that there was synchronisation in the initiation and development of vegetative flushes and spikes (plate 4b). Flushes emerged from lateral branch apices and / or from buds in leaf axils. The spikes appeared within one to eight days after the emergence of the flush (leaf) from sheath. The flowering season also showed a pattern similar to flushing, which was extended for a period of two to three months. The peak period of flowering was in the months of June and July. Broad peaks of flowering were observed both in Panniyur 1 and Karimunda. In general, spikes at anthesis were most abundant during six to eight week period between mid June and early August. However, flowering could also be observed as late as September-October in Karimunda. Between the two varieties, flowering peaks were observed during the concurrent periods even though, flowering started six days later in Karimunda.

Since flushing and flowering were resulted after a period of dormancy, it could be suggested that carbohydrate reserve in the stem of laterals might be utilised as remobilising substances for the flushing, as reported in various crops (Joubert, 1986 in litchi., Pandey, 1988 in mango and Nagao *et al.*, 1994 in macadamia nut). The period after berry maturity appears to be important for the accumulation of shoot carbohydrate reserves as the dry weight accumulation of berries cease to increase after this period.

5.2.2 Leaf growth and development

The leaf lamina is the major photosynthetic organ of the plant to intercept sun light and the productivity of the plant directly depends on the chlorophyll bearing surface area (Wahid *et al.,* 1997). Evidences suggest that factors such as leaf area index, leaf orientation etc., have major influence on radiation harvesting processes and govern fruit growth and maturity in several fruit crops. In black pepper also, leaf area and the number of leaves could be major factors that influence the final yield. This is because, leaf acts as the source of assimilates to the spikes and the number of spikes are determined by the number of leaves, as hypothetically each leaf is capable of initiating a spike.

During the life span of a leaf, generally three distinct phases can be distinguished. Initially the leaf is a net carbon importing structure and remains so until photosynthetic activities are in full swing. This is the period of leaf formation related to leaf area increase. This is followed by a second period when the leaf becomes an asset to the carbon economy of the plant. This period begins after maximum rate of leaf expansion is reached, and is called photosynthetic maturity. During the third phase, the leaf progress in to a period of massive mobilisation and export of photo assimilates. This is the period of senescence, which is accompanied by a gradual decline in photosynthetic capacity (Catsky and Sestak, 1997).

A clear understanding of the transformation of leaves from an importing to an exporting organ is fundamental in ensuring the contribution of an individual leaf to the carbon economy of the whole plant (Turgeon, 1989 and Ram *et al.*, 1994). In the present study, leaf area development in Karimunda and Panniyur 1 showed a similar pattern both requiring about five weeks to complete its growth. In both the varieties, almost 90 per cent of growth were completed within 21 days itself. The growth pattern also was exponential till this period. So it can be assumed that black pepper leaves become autotrophic within about three weeks after initiation, when they attain more than 90 per cent of the total development.

From the results, it can be assumed that the period of leaf area increase or the first phase in black pepper is up to 21 days at which the leaf reaches photosynthetic maturity (fig. 2a-b). The second phase is from 21 days to berry maturity during which the berry accumulates biomass continuously for a period of about 180 days. The period of senescence or the third phase starts immediately after berry maturity.

Panniyur 1 recorded the maximum values with respect to individual leaf area and total leaf area of the plant. On account of the larger leaf area, it can be assumed that Panniyur 1 had a faster leaf growth rate per unit time.

Fresh and dry weights of leaf increased up to 50th day. There were ups and downs in these parameters after this stage. This could be because, the leaves have attained photosynthetic maturity and the biomass accumulated might have been partitioned to the spikes whenever the sink demand prevails. When the sink demand from berries increases, the translocation from leaves also increases and vice-versa.

The leaf production per lateral in a season was significantly higher in Karimunda compared to Panniyur 1. Shoukathali (1997) also reported that leaf production in Karimunda was significantly higher than Panniyur 1 at all stages of growth.

Canopy level variation in leaf production was observed in Panniyur 1, with the variety showing marked increase in leaf production towards upper canopy level. This indicates that light is a limiting factor in leaf production in Panniyur 1 and the higher light availability in the middle and upper canopy levels might have a positive effect on leaf production. The requirement of higher illumination for growth and productivity in Panniyur 1 has been reported earlier (Nambiar, 1978). However, in Karimunda, the canopy level variation in leaf production was not evident. This indicates the adaptability of Karimunda towards shade. The results obtained in the present study are also in line with the findings by Mathai and Chandy (1988) who observed higher number of leaves in laterals of upper parts of the canopy.

The leaf production in the laterals was completed by August first fortnight in Panniyur 1 and September first fortnight in Karimunda. Thereafter there was no leaf production. Reports of dormancy after active growth as observed in black pepper in the present study have also been reported in mango (Gujante *et al.*, 1977) and cashew (Haresh, 1989).

The time interval between production of successive leaves was more or less same in both Karimunda and Panniyur 1. However, the plastochron index for the production of successive leaves varied and showed an increasing trend. It can be assumed that the time interval required for initiation of successive leaves is more towards the advancing insertional levels from first to last.

5.2.3 Spike growth, berry set and development

The period of spike growth ranged from 35 to 42 days between the varieties studied. The pattern of spike growth was exponential till 21 days and then showed a linear growth pattern. In both the varieties, 90 per cent elongation was completed within 28 days. The maximum growth rate was between 2nd and 3rd week after initiation (fig. 5a-b).

Menon and Nair (1989) made similar observations in black pepper in which spike growth was exponential till 22nd day in Panniyur 1 and 25th day in

Karimunda. They also had reported that the maximum length of spike was achieved in 31.67 and 29.26 days respectively, in Panniyur 1 and Karimunda.

Sexual composition, which is the number of hermaphrodite, female and male flowers in a spike, is critical in determining the yield. Ultimately it is the hermaphrodite flowers that matters since they lead to better berry set in black pepper.

In the present study, sexual composition of spikes showed minimum variability between varieties and seasons. In both Panniyur 1 and Karimunda, almost 98 per cent of the spikes were constituted by hermaphrodite flowers and the rest by female flowers. Menon (1981) also made similar observation in the variety Panniyur 1 wherein about 97.0 per cent of the flowers were bisexual. However, in Karimunda all the flowers were hermaphrodite.

The duration from berry set to berry maturity was around 165 days in Karimunda and 180 days in Panniyur 1. The seasonal growth pattern of berry fresh weight, volume and dry weight were similar for both the varieties. Growth was initially slow and the fresh weight of berries then increased exponentially up to 75 days in Karimunda and 60 days in Panniyur 1. The most rapid rate of increase in fresh weight was observed between 45 and 75 days after berry set. About 75 per cent of the development of fresh weight and volume were achieved by 90 days after fruit set. After this, growth was linear and the rate of berry growth was relatively constant. The fresh weight and volume of berries reached a maximum at 165 to 180 days and thereafter there was only increase in dry weight for another 15 days.

The developmental growth pattern of black pepper berries observed in the present study can be divided into three phases. Phase 1 corresponds to early growth in a linear pattern up to 45 days after berry set. This is followed by a period of early berry development stage from 45 to 90 days in which berries show rapid growth. Phase 3 corresponds to late berry development stage from 90 to 180 days during which the growth rate is relatively low and gradually declining. Maximum berry fresh weight was achieved at the end of this phase when the berries attain maturity. The maturation phase was characterised by cessation of fresh weight increase and continuation of dry weight accumulation. However, there was no distinct transition that delineated between these developmental phases.

The above observations indicate that the berry development followed a single sigmoid growth pattern in black pepper. Pome fruits such as apple and pear typically exhibit sigmoid growth pattern with a single period of exponential fruit growth (Westwood, 1993). In contrast, berries and drupes, typically exhibit double sigmoid growth curves, where a phase of minimal development separates two periods of exponential fruit growth (Monselise, 1986). However, in the present study, eventhough the fruit in black pepper is a drupe, only single sigmoidal growth pattern was observed.

The berry fresh weight, dry weight and volume were significantly higher in Panniyur 1 compared to Karimunda. Higher berry volume and weight have resulted in bolder berries in Panniyur 1. Genotype is often a dominant factor affecting fruit size (Broun *et al.*, 1985). This variety is having comparatively larger leaf area. Larger cross sectional area of phloem usually seen in larger leaves facilitated the translocation of source reserves compared to smaller leaves (Gardener *et al.*, 1985). The number of xylem vessels in the leaves of Panniyur 1 also was reported to be high (Thankamani, 2000). Probably this may be the reason for the bolder berries in Panniyur 1.

5.2.4 Extension growth of laterals

Growth of laterals is another important factor in black pepper as the stored foods present in them play a very crucial role in the spike initiation and development. The rate of growth will be proportionate to the quantity of food stored in the laterals.

Total annual extension growth of plagiotropes in the variety Karimunda was significantly higher compared to Panniyur 1. The past season length of lateral shoots at pre-flushing stage (table 1c) also was higher in Karimunda (10.12 cm) compared to Panniyur 1 (5.93 cm). This was increased by 19.46 cm in Karimunda and 14.75 cm in Panniyur 1 during the season. Menon (1981) observed an annual extension growth of 10.27 cm in the variety Panniyur 1. However, the mean extension growth was higher than this, in the present investigation. This also indicates that the extension growth of laterals vary between years.

Shoot growth commenced during flushing in June with the unfurling of the first leaf at the shoot tip. The growth duration of laterals was approximately 13 weeks in the varieties (fig. 9a-b). The growth rate showed an exponential trend till seven weeks and then became slow and the rate was declined finally. The shoot growth was continuous for a period of 13 weeks after which the vines undergo a period of dormancy and rest till the next rainy season.

After flushing, there was simultaneous expansion of leaf, growth of internode and initiation and growth of spike (plate 10a-b). Successive initiation of leaves and continuation of extension growth through internode elongation followed this. These sequences of events are repeated over successive cycles of growth. Simultaneously, the axillary buds in the older leaves just below the shoot tip also may get activated, and produce flushes and extension growth of internodes resulting in sympodial growth. Thus, extension growth is also resulted through axillary shoots and branches produced on the laterals (plate 11). In older vines, extension growth and branching of laterals mainly contribute to the annual growth. In such vines, new laterals are produced only in the top portion of canopy where the climbing shoots are always in active growing stage.

Black pepper exhibits a sylleptic type of branching in which there will be simultaneous sprouting of terminal as well as lateral buds. This seems to be on adaptive mechanism by the vine to produce maximum vegetative growth when the conditions are favourable.

5.3 Character of laterals at berry maturity

The average number of leaves per lateral was significantly higher in Karimunda while the individual leaf area and leaf area per lateral was significantly higher in Panniyur 1. The response of the varieties to the canopy levels were opposite to each other with Karimunda producing more leaves, average leaf area and total leaf area in the laterals of lower canopy and Panniyur 1 producing more number of leaves and leaf area in the upper canopy (fig. 10a-b).

Eventhough the variety Karimunda recorded more number of leaves per lateral, the higher leaf area of laterals observed in Panniyur 1 in the present study was due to the significantly higher average leaf area. The production of more number of leaves in Karimunda and higher leaf area in Panniyur 1 were endorsed in a study by Shoukathali (1997) in black pepper. The upper canopy levels in Panniyur 1 might have recorded more leaf area because of higher light availability and the positive response of the variety to light. Such a response was not observed in Karimunda, which also shows the adaptability of this variety to shade.

The length of internodes was more in Panniyur 1 while the number of nodes was more in Karimunda. More number of leaves was produced in the laterals of Karimunda during a season and this might have resulted in more number of nodes in this variety.

5.4 Biomass accumulation and partitioning

High crop yield is determined *inter alia* by the ability of a plant to produce a high level of photo assimilates and to partition a large proportion of that assimilates efficiently into harvested organs (Daie, 1985). In many crops, total dry matter and yield are positively correlated (Ankaiah and Rao, 1983). Since black pepper is sold on dry weight basis, accumulation of dry weight in the berries assumes importance, in terms of economic yield.

At berry maturity stage, total lateral fresh weight and dry matter accumulated in the current season growth of the lateral were significantly higher in Panniyur 1 compared to Karimunda (fig. 12a-b). The fresh weight and dry weight of the component organs such as stem, leaf and berry also followed the same trend. The dry weight per unit length of lateral also was higher in Panniyur 1. The accumulation of higher fresh weight and dry weight in the laterals of Panniyur 1 was resulted due to the higher accumulation of assimilates in the individual organs of the lateral such as the stem, leaf and spikes. The higher accumulation of dry matter in berries of the variety Panniyur 1 compared to

Karimunda was reported by Shoukathali (1997). The present results corroborate this finding.

In the present study, dry matter production in the lower part of the canopy was comparatively less and the laterals from the upper canopy levels accumulated higher fresh weight and dry weight especially in the variety Panniyur 1. This is partly in agreement with the results obtained by Mathai and Nair (1990) in black pepper wherein they observed no significant difference in dry weight of leaves among the canopy levels while the stem dry weight and berry dry weight were significantly higher in the upper parts. The lower dry matter production in the basal canopy may be because of the poor light availability and consequent reduction in dry matter. Thus, it can be assumed that in Panniyur 1, the canopy levels influenced partitioning and this may be due to the variation in availability of light at various canopy levels.

The distribution of dry matter into vegetative and reproductive organs of the lateral at berry maturity also showed varietal variation. Fresh weight and dry weight partitioned to leaves and stem of the laterals were high in Karimunda while the partitioning of assimilates to the spikes was the highest in Panniyur 1. The upper canopy spikes partitioned more dry weight compared to the lower levels. The partitioning was in the increasing order of stem, leaf and spike in Panniyur 1, while the order was stem, spike and leaf in Karimunda. The fraction of dry matter allocated to berries from berry set to harvest stage was 59.13 per cent in Panniyur 1 and 39.10 per cent in Karimunda.

The total biomass production and partitioning of greater fresh and dry matter into spikes amply indicates the superiority of Panniyur 1 in productivity. However, the dry matter partitioned to stem was less in Panniyur 1. After berry maturity, the sink strength of berries are less and the competing sink can probably be the stem. So the storage of photo assimilates after berry maturity is to the stem. This is stored during the dormant period and possibly remobilized for initiation of fresh growth activity and flushing during the subsequent season. In Karimunda, the dry matter partitioned to the leaf and internodes were higher indicating poor partitioning to berries. The higher accumulation of dry matter in the stem and leaves of laterals in Karimunda enable them to develop more flushes and flowers during the subsequent season.

This analysis leads to the conclusion that dry matter production and partitioning are two important factors of productivity in black pepper. Only when these two occur satisfactorily, higher productivity can be achieved, as in Panniyur 1.

5.5 Spike and yield characters

Spike length, number of developed berries and total berries per spike and hundred berry weight and volume were significantly higher in Panniyur 1 (fig. 15a-d). However, the number of spikes per vine was significantly higher in Karimunda. The spike weight and green and dry pepper yield were significantly higher in Panniyur 1 (fig. 16a-d). The upper part of the canopy was more productive in both the varieties with respect to characters contributing to yield and dry pepper yield. Shoukathali (1997) also had reported that dry pepper yield was 39 per cent more in the variety Panniyur 1 compared to Karimunda. Panniyur 1 had longer spikes, higher average berry weight and this might have contributed to the higher yield. The number of spikes produced in the laterals is significantly higher in Karimunda. This seems to be a varietal character.

More number of leaves and spikes, developed berries and berry dry weight observed in the upper canopy might have contributed to the higher dry pepper yield in the upper canopy. These attributes decreased as the leaf area exposed to illumination decreased towards lower parts of the canopy.

The effect of canopy level on spike production is evident from the fact that Karimunda, which is relatively tolerant to shade, produces spikes in the middle canopy on par with that of upper canopy. But in Panniyur 1, which requires open condition, produces maximum spikes in the upper canopy. Mathai and Chandy (1988) also had reported that spike production was more in the upper parts of the canopy in black pepper.

It can be concluded that the upper part of the canopy is more productive. This may be because, the upper part of the canopy is more exposed to sunlight, which might have resulted in more number of spikes and more number of developed berries.

5.6. Physiological parameters

There was no significant difference in specific leaf area, specific leaf weight and specific gravity of berries between the varieties. The leaf weight ratio and spike to leaf ratio was more in Karimunda.

A higher leaf weight ratio recorded in Karimunda implies that the dry matter production per unit leaf area is higher in this variety. This also had a higher spike to leaf ratio indicating more chances of producing spikes from every leaf axil. However, the dry pepper yield was higher in Panniyur 1. This may be due to the fact that the total leaf area per lateral was more for Panniyur1 and the spike length and dry weight partitioned to berries were also more. The study indicates that these physiological parameters are not dependable in assessing the productivity of black pepper genotypes.

5.7 Gas exchange parameters

Photosynthesis is the net result of various sub components and is dependent on various other physiological processes (Caemerer and Furquhar, 1981). Portable photosynthetic systems are useful in analysing the variation in photosynthetic rate and other components of leaf gas exchange in the field and their likely significance for crop yield.

Canopy photosynthesis is an important physiological determinant of crop yield (Gifford *et al.*, 1984 and Daie, 1985). Leaf lamina is the major photosynthetic organ of the plant and there has been instances wherein a good correlation between leaf photosynthetic rate and yield has been reported in various tree species (Daie, 1985., Muthuchelian, 1992 and Lawler, 1995).

In black pepper, the position of the inflorescence on the stem determines the source of photo assimilate to the particular inflorescence. The spikes are produced in leaf axils and the subtending leaf itself acts as the chief source of photosynthates to the spike (Mathai *et al.*, 1989 and Krishnamoorthy *et al.*, 2000).

Hence the flag leaf was used for analysing the photosynthetic parameters at different developmental phases of laterals in varieties Karimunda and Panniyur 1.

5.7.1 Photosynthetic rate

The results indicated that there was varietal variation in photosynthetic rate (fig. 17a). Among the different canopy levels, the photosynthetic rate increased significantly towards upper canopy levels. Among the stages observed, the period of flushing and flowering coincided with maximum photosynthetic rate in both the varieties tested. After berry set, this was declined and showed a fluctuating trend. Irrespective of variety and canopy level, leaves on spike bearing laterals had about double the average photosynthetic rate than the leaves that do not bear spikes (fig. 17b). Among the varieties, Panniyur 1 recorded an overall higher average of leaf photosynthesis during the entire season. Significant variation in photosynthetic rate among genotypes as observed in the present study also has been reported in cashew (Palanisamy *et al.*, 1994 and Latha, 1998) and asparagus (Bai and Kelly, 1999 and Faville *et al.*, 1999). Some reports have also inferred a link between leaf area and photosynthetic efficiency of leaves in the laterals of black pepper (Mathai *et al.*, 1989). Thus, the higher photosynthetic rate observed in the leaves of Panniyur 1 could also be attributed to the larger leaf area.

The lower photosynthetic rate recorded in the lower canopy level in the varieties may be due to the shaded condition and reduced light availability to the leaves due to self shading and mutual shading by adjacent vines. The higher photosynthetic rate observed in the laterals of middle and top canopy levels may be due to higher light availability. Similar reports are available in other crops. In cashew, Palanisamy and Yadukumar (1993) reported considerable variation in photosynthetic rate and PAR among the different canopy levels and observed the lowest photosynthetic rate in the bottom layers of the tree.

In the present study, the maximum photosynthetic rate was observed during the flushing and flowering stage. In black pepper, new flush, internode and the spike expand concurrently. These create an increased sink demand requiring additional photosynthates to sustain shoot extension and leaf expansion. Such demand of sink has been found to trigger net photosynthetic rate of leaves. The initially high photosynthetic rate recorded by black pepper leaves in the present study is typical of that found in a range of organs undergoing rapid expansion and is reported in several crops. In cashew, Palanisamy and Yadukumar (1993) reported that the transition from dormant stage of buds to flushing and flowering was characterised by a spurt in photosynthetic rate of leaves. Similar increases in photosynthetic rate occur at bud burst in tea (Botwright *et al.,* 1998). Seasonal variation in photosynthetic rate was also reported in cocoa (Balasimha, 1999) and asparagus (Bai and Kelly, 1999).

After spike development is over, the photo assimilates synthesized by the flag leaf would be sufficient in maintaining the fruit development. At the time of berry set, berry development and berry maturity, the additional leaves formed in the current season will also contribute to the photosynthetic pool, which will be sufficient to meet the sink demand so that additional assimilates from increased photosynthesis are not required. Towards berry maturity, the berries stop accumulating biomass and hence the photosynthetic rate showed a declining trend. However, photosynthetic rate of leaves remains stable and the photo assimilates synthesized are transported and stored in the nodes and inter nodes of the lateral which act as reserves during quiescence.

Among arecanut, cocoa, cashew and coconut, cashew had higher net photosynthesis of 8.21 μmol m^{-2} s^{-1} (Rajagopal and Balasimha, 1994). Latha (1998) reported that the net photosynthetic rate of cashew varieties ranged between 3.880 μ mol m^{-2} s^{-1} and 9.551μ mol m^{-2} s^{-1}. Photosynthetic rate of *Pterocarpus marsupium* and *Ailanthus triphysa* were 8.4 μ mol m^{-2} s^{-1} and 3.4 μ mol CO_2 m^{-2} s^{-1} respectively (Rajesh, 1996). The seedlings of *Acacia auriculiformis* had a net photosynthetic rate of 11 μ mol CO_2 m^{-2} s^{-1} under regular watering (Somen, 1998). The average leaf photosynthetic rate obtained in the present study in black pepper is between 1.842 to 2.001 μ mol CO_2 m^{-2} s^{-1}. These rates are low compared to other C 3 plants. This can be explained in the context of the report that leaves with longer duration of life usually have lower net photosynthetic rate with less pronounced maxima and the development of photosynthesis is extended over a larger time scale (Catsky and Sestak, 1997).

Positive association between leaf photosynthetic rate of the varieties and yield are observed in black pepper. Therefore, this parameter can be considered as an indicator of selection in breeding programmes.

5.7.2 Stomatal resistance (r_s) and transpiration

These two parameters are important in black pepper as they give some indications in selection for stress tolerance (Vasantha *et al.*, 1990). Stomatal resistance was significantly higher in Karimunda and the lower canopy levels recorded more r_s especially in Karimunda. Stomatal resistance was highly fluctuating between stages and was lower towards berry maturity stage (fig. 18a-b)

The general means of r_s values for Karimunda and Panniyur 1 obtained in this study did not show much deviation from the r_s values obtained by Vasantha *et al.* (1990). She had reported that Panniyur 1 showed lower r_s and higher transpiration indicating its inability to respond to relatively severe stress compared to Karimunda.

Canopy level variation in r_s observed in the present study may be due to the variation in light and temperature observed in the different canopy levels. In cashew, the transpiration rate observed in the lower part of the canopy was significantly less compared to that of the upper canopy (Palanisamy and Yadukumar, 1993).

The lower r_s values recorded towards berry maturity period may be due to the lack of rainfall and reduced soil moisture during this period. Krishnamurthy *et al.* (1998) also had reported that stomatal resistance decreased and transpiration rate increased with water stress intensity in black pepper.

The transpiration rate was higher in Panniyur 1 compared to Karimunda at all canopy levels and type of laterals (fig. 19a-b). Leaves from the upper canopy recorded higher transpiration rate. The trend in the variation in transpiration rate during the various stages was similar in both varieties, indicating seasonal and climatic effects. The variation in transpiration rate of varieties in relation to the stages observed was not consistent.

Similar observations were made in a study on drought tolerance of black pepper (Vasantha, 1996) in which the variety Panniyur 1 showed higher transpiration compared to other varieties indicating its inability to respond to relatively severe stress. Thankamani (2000) also had reported that the transpiration rate showed variation depending on varieties and water stress levels and higher rate of transpiration was observed in Panniyur 1. In cashew also, the transpiration rate differed considerably among varieties (Latha, 1998). Variation in transpiration rate among genotypes was also reported in coconut (Rajagopal and Balasimha, 1994).

The variation in stomatal resistance and transpiration observed in the present study at different stages may be due to the different levels of stress prevailed during the development of laterals and leaves. Krishnamurthy *et al.* (1998) also had reported that in black pepper, stomatal resistance increased and transpiration rate decreased with stress intensity in the genotypes. In cashew, transpiration rate has decreased during dry periods with decreased soil moisture (Latha, 1998). Seasonal variation in transpiration was reported in cocoa also (Balasimha, 1999).

5.7.3 Leaf surface temperature

Enzymatically controlled CO_2 fixation is dependent on temperature. Increasing temperature strongly influences the photosynthetic capacity of leaves with the exception of C 4 plants and photorespiration (Wahid *et al.*, 1997). In the present study, the leaf surface temperature recorded by Panniyur 1 was significantly higher in the entire canopy level and stages observed. The top canopy had higher leaf temperature compared to the other two levels. There was a gradual increase in leaf temperature as the season advanced from flowering to harvest.

There was not much variation in leaf temperature between genotypes in black pepper at non stress levels (Thankamani, 2000). This is in contrast to the results obtained in the present study. Similarly, there was not much variation in leaf temperature among different genotypes in coconut (Jeyakumar and Giridharan, 1998). However, in cashew, the leaf temperature considerably differed among varieties (Latha, 1998).

The higher leaf temperature observed in the top canopy may be because of more exposure to sunlight. Similar reports are available in cashew in which the leaf temperature in the lower part of the canopy is lesser (Palanisamy and Yadukumar, 1993).

The increase in leaf temperature observed as the season advanced may be due to the seasonal change in atmospheric temperature.

5.7.4 Photosynthetically Active Radiation (PAR)

The photochemical reaction of photosynthesis is dependent on light fluctuations. With a gradual increase in light intensity, there is a relatively larger increase in photosynthesis up to light compensation point. With further increase in light, there is a relatively small increase in the photosynthetic rate of C 3 plants (Wahid *et al.*, 1997). The study revealed that varieties differed in their response to light illumination and the PAR recorded at leaf surface was higher in Panniyur 1 compared to Karimunda. The top canopy level recorded maximum PAR in leaf surface. The spike bearing laterals recorded higher PAR compared to laterals without spikes (fig. 21a-b).

The light compensation point in Panniyur 1 was higher compared to Karimunda indicating that the variety can fix increased carbon at higher light intensities. So this variety will be more productive under increased illumination. Also, the laterals in Panniyur 1 is likely to receive more light at all canopy levels as the variety has a less compact canopy and the laterals are more protruded and exposed to light compared to Karimunda. Mathai and Chandy (1988) made similar observation in black pepper. The photosynthetic response in black pepper was largely saturated at low light intensities and PAR below 300 μ g m^{-2} s^{-1}. This indicates that the leaves would be adapted to low light environment. From the low light compensation point observed in the present study, it can be assumed that black pepper in general is adapted to shaded conditions.

The higher PAR recorded in the leaves of the upper canopy may be because the vines are more exposed in the top canopy and they are subjected to more light compared to the lower levels. Similar observations were made in cashew by Palanisamy and Yadukumar (1993) in which the PAR was higher in the upper part of the canopy.

5.7.5 Vapour Pressure Deficit (VPD)

The results showed that VPD was significantly higher in the leaves of Panniyur 1 compared to Karimunda. The middle canopy levels had lowest VPD and top canopy had the highest. VPD was highly fluctuating among the stages observed (fig. 22a-b).

The fluctuating nature of VPD during the various stages may be due to the variation in seasonal and environmental parameters especially the soil moisture status. The lower VPD in the mid canopy level indicate that the stress level induced on the leaves in different parts of the canopy is not uniform.

Stomata normally close in response to increase in VPD affecting photosynthesis. This could be one of the reasons for fluctuation in photosynthetic rate observed during different stages.

5.7.6 Stomatal conductance

Stomatal conductance also followed a similar trend to that of photosynthetic rate. The g_s recorded by the leaves in Panniyur 1 was more compared to Karimunda. This was lower in the basal canopy and showed an increasing trend in the middle and upper canopy levels. Among laterals, spike-bearing laterals recorded significantly higher g_s irrespective of canopy levels or varieties. Stomatal conductance was the maximum during flushing and flowering stage in Panniyur 1 and during early berry development stage in Karimunda. There was a general declining trend in g_s values as the season advanced towards December.

In the present investigation, stomatal conductance varied between varieties (fig. 23a). Thankamani (2000) also obtained similar results in which Panniyur 1 recorded more stomatal conductance than other varieties. Variation in stomatal conductance among genotypes is also observed in cashew (Latha, 1998). Canopy level variation as observed in the present study has also been reported in cashew. Palanisamy and Yadukumar (1993) reported that leaves from the lower canopy have lesser g_s compared to the upper canopy.

The comparatively lower g_s values recorded towards the maturity period of the berries may be due to the stress condition induced by higher temperature and low soil moisture status consequent to the climatic conditions. Similar reports are available in cashew in which there was drastic decline in g_s with increase in the duration of stress (Latha, 1998). In cocoa also, Balasimha (1999) reported seasonal variation in stomatal conductance, which got decreased with increased water stress during summer months.

The decline in g_s during the latter part of the season also may be due to the aging of leaves. Ekanayake *et al.* (1994) reported that g_s declined in older banana leaves, as a result of leaf senescence.

The ratio of assimilation rate (A) per unit stomatal conductance (A / g_s) is often considered as a reflection of the intrinsic water use efficiency (WUE) of the genotype. A / g_s relationship is an informative tool on how stress may influence photosynthetic rate and water use efficiency. This is also useful in determining the optimum leaf area index and canopy size.

The results indicated that there was generally a linear relationship between leaf photosynthetic rate and g_s values. This suggests that difference in stomatal conductance between varieties and laterals contribute significantly to the variation in photosynthetic rate. Positive correlation between photosynthesis and g_s was also reported in three species of tree crops (Gurumurthy, 1994) and asparagus genotypes (Bai and Kelly, 1999).

Though there was difference in A between the variety Panniyur 1 and Karimunda, there was no variation in the overall A / g_s ratio, a reflection of water use efficiency. Spike bearing laterals and laterals with out spikes and canopy levels also did not differ significantly in A / g_s relationship. The developmental stages also showed similar A / g_s relationship between varieties except flushing.

5.7.7 Sub-stomatal CO_2 concentration (Ci)

The variety Karimunda recorded higher Ci in the leaves compared to Panniyur 1 and the upper canopy level recorded significantly higher Ci compared to the basal canopy. The Ci recorded at the various stages also was different (fig. 24a-b).

The results obtained in this study are in contrast with the findings of Palanisamy and Yadukumar (1993) in cashew, in which the lower canopy recorded higher Ci compared to middle and top canopy levels. This may be because in black pepper, the canopy structure is different from that of cashew, which has a closed canopy. The variation in Ci at different stages may be due to the variation in CO_2 in the atmosphere.

In studies where photosynthetic rate was measured at saturating light intensities, a significant increase in A with increase in Ci has been shown. Elevated ambient CO_2 can result in an increased A due to an increase in internal partial pressure of CO_2 (Ci) in the leaves (Caemmerer and Furquhar, 1981). The elevated CO_2 concentration on the upper part of the canopy might have resulted in higher photosynthetic rate of leaves as observed in the present study.

The ratio of A to unit intercellular CO_2 concentration (A / Ci) is considered as an indirect reflection of the carboxylation efficiency (Kumuda, 1991). The variety Panniyur 1 has recorded an overall higher A / Ci ratios compared to Karimunda and thus might have a higher photosynthetic efficiency.

5.8. Biochemical parameters

The transformation from vegetative to reproductive phase has been reported to change the status of biochemical constituents in plants. Analysis of plant extracts for various biochemical constituents, therefore help in better understanding of the metabolism and productivity. Several researchers have emphasised that the plant part or age determines the level and nature of endogenous constituents.

In black pepper, since the flag leaf acts as the chief source of photo assimilates to the subtending spike (Mathai *et al.*, 1989 and Krishnamurthy *et al.*, 2000) it was sampled for analysing the biochemical constituents at different developmental phases of laterals.

5.8.1 Chlorophyll content

The ontogeny of photosynthetic development in leaf is associated with numerous events, which include the pigment accumulation. In the present study, a rapid increase in pigments during the leaf ontogeny was observed in both the varieties. Such increase in chlorophyll concentration with leaf ontogeny has been reported earlier (Sestak, 1966). In banana, Thomas and Turner (1998) also reported significant increase in leaf chlorophyll content until the leaves were at least 17 days old and attained 80 per cent of its maximum value when they were seven days old.

The pattern of development of chlorophyll in the leaves from the day of unfurling to 35 days after opening indicated that the chlorophyll development was faster in Panniyur 1, as the chlorophyll content recorded till fourth week after opening was significantly higher in this variety (Fig. 25a). This shows that the leaves of Panniyur 1 become autotrophic at an earlier stage than Karimunda. However, on the fifth week, Karimunda and Panniyur 1 was on par with respect to the contents of chlorophyll 'a', 'b' and total of the leaves. The peak chlorophyll content was observed at 35 days after flushing.

During the various developmental phases of the lateral, the chlorophyll ('a', 'b' and total) contents were on par between the varieties tested at all canopy levels except the middle canopy. The leaves of Karimunda recorded significantly higher chlorophyll content at the mid canopy level. In both Karimunda and Panniyur 1, the content of chlorophyll 'b' was higher in leaves compared to chlorophyll 'a'. The result of the present study partly agree with the earlier reports in black pepper (Thankamani, 2000). Latha (1998) and Pushpalatha (2000) also reported varietal variation in chlorophyll content of leaves in cashew. These results showed that the chlorophyll content expressed on fresh weight basis differed significantly between seasons and varieties.

Leaves from the middle canopy recorded significantly higher chlorophyll 'a', 'b' and total contents compared to basal and upper canopies. This may be due to the fact that light and temperature received by the middle canopy are comparatively lesser and resulted in more accumulation and less degradation of chlorophyll. Similar reports are available in hazelnut in which shading altered leaf chlorophyll concentration and chlorophyll a/b ratio. Mean chlorophyll concentration was 157 per cent higher on dry weight basis of leaves in 92 per cent shade, than in full sun (Hampson *et al.*, 1996).

The chlorophyll content of source leaves at various developmental phases of the lateral indicated significant difference among the stages observed. The chlorophyll content was the maximum during berry development stage in both Panniyur 1 and Karimunda (fig. 25b). A decrease in chlorophyll content was noticed towards berry maturity and harvest. The period of berry maturity and harvest coincide with rise in atmospheric temperature (November-December). Such reduction in chlorophyll content under high temperature and drought condition was reported earlier in tea (Rajasekar *et al.*, 1991) and black pepper (Thankamani, 2000). Seasonal variation in chlorophyll content of leaves with the changes in environmental factors has been reported in many crops. The chlorophyll content in leaves varies with temperature, irradiance and radiation quality and nutrient status of soil (Lewandowska and Jarvis, 1977 and Spyropoulose and Mavrommatis, 1978). The chlorophyll content of different tree species varied from month to month and also from one species to another (Naidu and Swamy, 1995). The decrease in chlorophyll content of leaves during berry maturity and harvest stage as observed in the present study also may be due to the leaf age as it was advancing towards senescence.

Spike bearing laterals recorded more chlorophyll content compared to laterals without spikes. The higher content of chlorophyll in the leaves of spike bearing laterals coupled with light availability and increased photosynthetic rate might have resulted in spike formation in the laterals.

5.8.2 Carbohydrate content

Carbohydrates synthesised in the plants are used as structural compounds for respiration or stored as organic acids and sugars in the vacuoles. These structural compounds are invested in the growth of the whole plant.

In all the stages, Panniyur 1 dominated and maintained significantly higher leaf carbohydrate compared to Karimunda (fig. 26a). The accumulation of carbohydrate was highest in the lower canopy in Panniyur 1, while there was no variation in the canopy levels in Karimunda. The carbohydrate content also varied significantly among stages. The total carbohydrate content of leaves increased from flushing and flowering to berry set and then decreased during berry development stage. This again showed an increasing trend towards berry maturity and reached the maximum at the harvesting stage of spikes in the lateral. Spike bearing laterals accumulated more carbohydrates compared to laterals with out spikes (fig. 26b).

Variation in the carbohydrate content of leaves among varieties has been reported in black pepper by Shoukathali (1997) and Thankamani (2000). Daggade (1999) reported higher content of non-reducing sugars in the leaves of Panniyur 1 compared to the other varieties. In cashew also, Pushpalatha (2000) had reported high carbohydrate content of leaves in high yielding varieties. Varietal variation on the relationship between starch content and flowering was observed in apple (Yang and Wang, 1994).

The higher carbohydrate accumulation in the leaves of Panniyur 1 observed in the lower canopy may be due to the lower level of translocation as the productivity of the lower canopy was less due to shaded condition.

The seasonal trends in total carbohydrate content of a plant reflect the acquisition of carbon through photosynthesis, its utilisation for synthesis and maintenance of biomass and regeneration of reserves consumed in growth. In perennial crops generally, maximum carbohydrate level occur before flowering and decline to a minimum during shoot growth, flowering and fruit development. Accumulation begins at the time of maturity and harvest and continues until the next floral initiation (Whiley *et al.*, 1989). The results showed that the pattern of development of carbohydrates in the leaves of black pepper is also in line with the above findings.

For both Panniyur 1 and Karimunda, the pattern of carbohydrate accumulation in leaves was similar during the various stages observed. Minimum concentration of carbohydrates in leaves was observed during flushing and flowering, which is the most active period of reproductive growth. Leaf carbohydrate level showed an increasing trend from flowering to berry set, then it declined during berry development and again increased up to maturity and harvest stage. Relatively lower values of leaf carbohydrate during flushing and berry development can be associated with the increased sink demand during flushing and berry development. So this might have resulted in increased translocation of assimilates during berry development from the leaves to the berries. Mathai *et al.* (1988) observed that berry growth after 45 days of initiation was dependent on current photosynthates for its dry matter accumulation. Lower levels of carbohydrates at the time of flushing and fruit development as observed in the present study is in agreement with the findings of Shoukathali (1997) in black pepper and various fruit trees (Stephenson *et al.,* 1989). Seasonal fluctuation in the carbohydrate level of leaves and shoots during development phases and seasons was reported in avocado (Scholefield *et al.,* 1985), apple (Broun *et al.*, 1985) and peach (Stassen *et al.*, 1981).

It was reported that the removal of source leaf subtending the spike from the laterals in black pepper 60 days after spike initiation affected the yield attributes (Krishnamurthy *et al.*, 2000). So it can be assumed that the low level of total carbohydrates in the leaves during berry development stage reflected the increased demand for carbohydrates from the leaves during this stage also.

The leaf carbohydrates accumulated during maturity and harvest period indicates that carbohydrate transport out of leaves may be lagging behind the rate of photosynthesis. This may also be due to reduced sink demand for assimilates.

Shoukathali (1997) has also reported similar accumulation of carbohydrates in the leaves of black pepper towards harvest stage. Carbohydrate accumulation after maturity and harvest is common in many plants (Pandey, 1988). This also indicates reduced requirement of carbohydrates by berries during final stage of maturation. During berry maturity and harvest stage it is possible that current photosynthates by spikes and berries themselves could help in their maintenance.

5.8.3 Phenol content

Phenols are known to have multiple action on plant metabolism. They are reported to stimulate flowering in short day plants (Kumar, 1979 and Bernier, 1988). They have active role in the biosynthesis of essential oil and piperine content in the berries of black pepper (Shoukathali, 1997).

The phenol content of leaves varied significantly among the stages observed in both Panniyur 1 and Karimunda (fig. 27a). The content was higher in Karimunda during berry maturity and harvesting stage. Phenol content was significantly higher in the leaves sampled from top canopy level. Similarly, the leaves from spike bearing laterals had significantly more phenol content compared to those without spike (fig. 27b).

Varietal difference in phenol content of leaves in black pepper has been reported earlier by Daggade (1999). He had observed that the variety Kalluvally recorded higher total phenol content (3.245 mg g^{-1}) compared to Panniyur 1 (2.123 mg g^{-1}). In grapes, Giridharan (1993) also observed that the total phenol content varied between varieties.

The phenol content in the leaves of spike bearing laterals was high in the present study. Similar reports are available in mango (Patil *et al.*, 1991), in which the shoots that transform into fruit buds showed higher level of phenols.

The lowest level of phenol was observed during the flushing and flowering stage of laterals. After this, the phenol content of leaves was almost constant till the berry development stage. The lower level of phenols at flushing and flowering may be due to the fact that certain phenols may get degraded to promote flowering. They may also be utilised for the build up of secondary metabolites like oleoresin and essential oil in the berries during berry development stages. At berry maturity and ripening, phenols might have started accumulating in the leaves, as they are not utilised by the berries at these stages.

5.8.4 Amino acids

The amino acid content of leaves differed significantly among developmental phases of the lateral. The content was the highest during flushing, flowering and spike development. Thereafter it showed a declining trend. The top canopy level had significantly higher level of amino acid content compared to lower canopy. The spike bearing laterals had significantly higher content of amino acids (fig. 28a-b).

Daggade (1999) reported varietal variation in amino acid content of leaves in black pepper. He had observed that the variety Kalluvally had higher content of total free amino acids (0.035 mg g^{-1}) compared to Panniyur 1 (0.30 mg g^{-1}). However, the varieties did not differ significantly in the amino acid content of leaves in the present study. This may be due to the fact that inter conversion of amino acids to primary products (carbohydrates) might have occurred in Panniyur 1 which facilitated the plant to accumulate more carbohydrates.

The higher concentration of amino acids observed in the present study during flushing and flowering could be explained in the context of findings in mango by various workers. Rao *et al.* (1982) reported increased concentration of total free amino acids in the leaves at flowering stage in mango. Sreehari (1995) also reported increased trend in the accumulation of amino acids throughout the flower bud differentiation process.

The amino acid content declined towards maturity and harvest periods of berries in the lateral. This may be due to the reason that water stress levels might have increased during this period and resulted in breaking up of amino acids. Such reduction in amino acids in black pepper varieties under stress conditions has been reported by Thankamani (2000).

There was negligible change in the amino acid content in the leaves without spikes except during berry maturity and harvest stage. The amino acid content dropped to 189 mg g^{-1} and 179 mg g^{-1} respectively, during these stages while there was a steep rise in the amino acid content of spikes with laterals during flushing and berry development stage. Similar trend was also reported in mango by Sreehari (1995).

5.8.5 Seed protein electrophoresis

Proteins as primary gene products are good markers of genetic variation and seed protein electrophoresis has been used as markers in the characterisation of crop genotypes.

The over all profiles of seed protein in Karimunda and Panniyur 1 observed in the present study have similarities in six bands and the variation is moderate. The differences in zymogram between Karimunda and Panniyur 1 appear to be in the number of bands and staining intensity of bands.

On the analysis of the electrophorogram, it was observed that the replications in Panniyur 1 showed the absence of intra-varietal variation in banding pattern, suggesting varietal homogeneity. However, in Karimunda, variations in the banding patterns of protein were noticed between replications, indicating intra-varietal variation. This may be because, Panniyur 1 is a hybrid evolved through breeding and have been multiplied clonally while Karimunda is a cultivar that was naturalized through seeds and later multiplied through vegetative means. The bands 1, 2, 4, 5, 7 and 8 were common to Karimunda and Panniyur 1.

The result of this preliminary study has shown that two extra bands are visible in the variety Panniyur 1. Since these are seed proteins, they contribute to the genetic material, which will influence growth and development of the vines. Seed is a miniature plant and hence, the hybrid vigour observed in Panniyur 1 in terms of the leaf area, spike length, bolder berries, dry matter accumulation and yield could be attributed to the two extra proteins present.

5.9 Translocation pattern of labelled photosynthates

Crop productivity depends on canopy size, photosynthetic efficiency of individual leaves and the extent of partitioning of photosynthates to economically important parts (Gifford and Evans, 1981). In order to improve productivity by manipulating photosynthate translocation, knowledge of the sink activity is necessary. Studies were conducted to obtain knowledge about the sink activity and the pattern of partitioning of photosynthates from the source leaf to the component organs of the lateral in bush pepper during four stages of development of a lateral.

The studies indicated that there was varietal variation in partitioning of photosynthates to various parts of the bush pepper plant. The pattern of partitioning also varied with the developmental stage of the lateral (Fig. 30a to h).

At flushing stage, when there is no subtending spike on the flag leaf in a lateral, about 97 per cent and 90 per cent of the photosynthates fixed were held back by the flag leaf itself in the variety Karimunda and Panniyur 1, respectively. Only the remaining photosynthates were effluxed out of the leaf within 24 hours of fixation. The lesser demand for current photosynhates during this stage could be due to the lack of an active sink, as the laterals were devoid of spikes. This might have resulted in the retention of photosynthates in the source leaf itself.

At flowering stage, which is characterised by initiation of spikes and growth of spikes in length, the varietal variation in partitioning was evident. While the developing spikes received only 9.33 per cent of the photosynthates in Karimunda, the influx of labelled carbon to the spikes in Panniyur 1 was as high as 57.53 per cent. The photosynthate held back by the fed leaf was 89.11 per cent in Karimunda while this was 39.8 per cent in Panniyur 1. The study has shown that, the variety Panniyur 1 is more efficient in translocating photosynthates to the economically important part, the berries. The lesser demand for photosynthates in the variety Karimunda during this active period of growth could be due to the lesser need for current photosynthates by the spikes. This low demand could be attributed to the remobilization of reserves from the stems, as the dry matter partitioned to stems was higher at harvest stage in this variety.

At berry set stage also, the pattern of partitioning was similar to the flowering stage. The variety Karimunda retained 72.48 per cent of the total photosynthates in the fed leaf itself and only 10.22 per cent were effluxed out to the spikes. In Panniyur 1 at this stage, spikes commanded maximum share (80.23

%) of the total radioactivity fixed by the plant, and the fed leaf retained only 16.13 per cent. It can be assumed that in the variety Karimunda, at the berry set stage, the relative sink strength by the spikes is not enough to mobilise current photosynthates. But in Panniyur 1, the relative sink strength by the spike and berries set is high enough to attract more photosynthates. The results of the study in bush pepper variety Panniyur 1 obtained by Thankamani (2000) corroborate these findings. She had reported that when the subtending spikes on the source leaf acted as a stronger sink, major share of photosynthates was translocated to the spikes in both stressed and unstressed plants.

At berry development stage, of the total amount of photosynthates effluxed out of the fed leaf, 32.32 per cent was utilized by the developing berries, 53.72 per cent by the stem of the laterals and only 12.72 per cent was retained by the source leaf in the variety Karimunda. However in Panniyur 1, the developing berries partitioned the maximum photosynthates (72.80 %) indicating a heavy sink strength at this stage also and 24.9 per cent was retained by the source leaf. Only a negligible quantity (0.25 %) was stored in the stem of the laterals.

During all the stages observed, only a minor fraction of the photosynthates was partitioned to the other aerial parts of the plant and roots. More than 90 per cent of the assimilates were shared by the leaf, spike/ berries and stem of the lateral, indicating that productivity of black pepper primarily depend on the laterals.

The study has shown that the amount of labelled CO_2 retained by the source leaf depends on the sink demand. In the variety Panniyur 1, the demand for current photosynthates is very high during flowering, berry set and berry development due to the increased sink activity and hence any factor detrimental to source activity during this stage can affect the final berry development and yield. In Karimunda, the most critical stage with respect to demand for current photosynthates is berry development stage. Thus it is indicated that the current photosynthate requirement of sink varied according to their stage of development and the genotype.

Varietal variation in the translocation of photosynthetic assimilates have been reported in black pepper (Mathai *et al.*, 1988) and other crops and its relationship with productivity has been shown (Austin and Longden, 1967). Between the two varieties, Karimunda had lesser partitioning efficiency to its spike and berries during flowering, berry set and berry development. The level of photosynthates stored in the source leaf decreased from flushing to berry development while the photosynthates partitioned to spike and berries increased from flowering (9.33 %) to berry development (32.32 %). The photosynthate partitioned by the stem of the lateral was the maximum in Karimunda (53.72 %) during berry development stage. This indicates that the photosynthates are stored in the inter nodes and leaves towards the advanced stage of berry development, which could be remobilised for flushing and flowering during the subsequent year. The higher accumulation of photo assimilates in the stem of the laterals in Karimunda towards the later period of development of berries enable them further to remobilise the reserves and to develop more leaves and spikes during the next season. This could be the probable reason why Karimunda performs to be more or less a regular bearer. However, in Panniyur 1, the partitioning efficiency of the spikes and berries were the maximum during flowering (57.53 %), berry set (80.13 %) and berry development (72.88 %). On the contrary, percentage of assimilates retained in the leaf (24.97 %) and the stem of the lateral (0.25 %) was comparatively low during the berry development stage. This indicates that the photosynthates generated during the current season are utilised for berry set and development and the storage in the internodes and leaves is less. This will probably explain the reason for alternate bearing tendency noticed in Panniyur 1.

5. 10 Correlation studies

Productivity of a plant is the ultimate reflection of the interaction between component characters and a complex of their direct and indirect effects, which are predominantly governed by the genotype, and the environment. In black pepper also, yield is the net result of an integrated set of complex characters, which are inter related. Therefore nature of correlation between dry pepper yield and the component characters assume significance in early selection for crop improvement.

The results of the correlation studies revealed that yield characters of the vines such as fresh weight of berries and spikes and the number of spikes registered significantly higher correlation with dry pepper yield. These were in conformity with the findings of Ibrahim *et al.* (1985 a) and Sujatha (1991). Since these characters are having direct influence on yield, such positive correlation could be anticipated.

Almost all the spike and berry characters also showed significant positive association with yield, the most important among them being number of developed berries and total number of berries in a spike and spike length. These findings are also in agreement with the reports by Ibrahim *et al.* (1985 a) and Sujatha (1991).

Among the characters of the lateral, total fresh weight and dry weight of the lateral had significantly high correlation with dry pepper yield. Fresh weight and dry weight of stem of the lateral also showed significant association with yield.

The relationship between biomass accumulated by the lateral and economic yield can be explained on the basis of the dual role played by them as source and sink during different developmental phases of the spikes and berries. During flushing and flowering, they act as the source of reserve carbohydrates which are remobilized to meet the excess sink demand by the developing leaves, spikes and berries. After berry maturity and harvest, the stem acts as the prominent sink. The results of the studies by Mathai and Nair (1990) corroborate this finding. This also shows the usefulness of these characters in early selection, which will give an indication of productivity even before bearing age. Based on this, screening of promising genotypes can be made at an early stage.

Inter correlation of characters also provided certain useful indications in selection. Leaf area of the lateral exhibited significant correlation with spike fresh weight and dry weight, number of developed berries and total number of berries in a spike. However, number of leaves in the lateral showed negative association with fresh weight and dry weight of spikes, number of developed berries in a spike and total fresh weight and dry weight of the lateral. This may be because when more number of leaves are produced, there may not be effective partitioning of biomass to the spikes, as a portion of the stored carbohydrates could be utilised for the initiation of new leaves. Similar positive association of leaf area with number of developed berries and total berries in a spike and length of spikes had been reported by Mathai *et al.* (1991).

It was observed that dry pepper yield was positively correlated with photosynthetic rates. Vasanthakumar (1986) in cardamom and Mathai *et al.* (1988) in black pepper also obtained positive correlation between biomass and photosynthetic rates, and berry yield. However, this is in contrast with the results reported by Latha (1998) in cashew wherein there was no correlation between photosynthetic rate and biomass yield.

The results suggest that the average seasonal photosynthetic rate of leaves in the lateral would be a good indicator of the yielding ability and can be included as a selection criterion in breeding programmes.

Among the biochemical characters studied, only chlorophyll and carbohydrates had significant correlation with yield. Positive correlation between leaf chlorophyll content, photosynthesis and biomass production have also been reported by Agarwal and Prakash (1980) in *Butea monosperma* and Naidu and Swamy (1995) in several tropical deciduous tree species.

Evidences to suggest positive correlation between carbohydrate content of leaves and yield are available in mango (Patil *et al.*, 1991), grapes (Giridharan, 1993) and cashew (Pushpalatha, 2000). Since chlorophyll and carbohydrates have shown positive correlation with economic yield, these characters also appear to be promising in selection. However, since the significance is only at five per cent level, a detailed study including large number of genotypes will be more useful in confirming the results.

Summary

SUMMARY

Investigations on 'Physiological and biochemical aspects of flowering, berry set and development in black pepper (*Piper nigrum* L.)' were carried out at Pepper Research Station, Panniyur and College of Horticulture, Vellanikkara, during 1997 to 1998. The varieties Karimunda and Panniyur 1, were selected for the study. The chronological events in the growth and development of the lateral were traced and the morphological, biochemical and photosynthetic parameters associated with growth and productivity were assessed and correlated. The biomass accumulation and partitioning to the components of the lateral and the photo-assimilate translocation and partitioning into various organs of the bush pepper were investigated. The results of the experiment are summarized below.

6.1 Chronological events in the growth and development of laterals.

Flushing commenced on 11th June in 1997 and 3rd June in 1998 and Panniyur 1 was early to flush. The leaf area development was completed in 35 days in both the varieties. However, 90 per cent of leaf growth was completed in 21 days. The leaf area constants for Karimunda and Panniyur 1 were 0.68 and 0.71 respectively.

The fresh and dry weights of leaf increased up to 50 days after opening and were significantly higher in Panniyur 1. Leaf production was significantly more in Karimunda and an increasing trend in leaf production towards upper canopy was visible in Panniyur 1. The plastochron index on an average was 23 days in both the varieties. Plastochron index increased as the insertional level of leaves advanced.

Flushing and flowering was synchronous and spike emergence was up to 6 days late in Karimunda and up to 9 days late in Panniyur 1. Further production of spikes occurred after the emergence of subsequent leaves.

Spike growth was completed within 35-42 days in the varieties and 90 per cent of the growth was attained within 28 days after initiation. The growth of spike was exponential till 21st day and thereafter it declined.

Sexual composition of spike did not vary significantly between varieties. Ninety eight per cent of the flowers were bisexual and the rest were female. No male flowers could be observed. No seasonal and canopy level variations could be observed with respect to the sexual composition of spike.

The fresh weight of spikes increased up to 150 days after berry set. The rate of increase in fresh weight was highest during the first month of berry set and thereafter it declined till berry maturity up to 150 days. Eighty per cent of the total fresh weight was gained within three months after berry set.

Number of spikes produced per lateral and per vine was significantly higher in Karimunda. Spike production showed an increasing trend from lower to upper canopy. Canopy level variation in spike production was more pronounced in the variety Panniyur 1.

The period from flowering to completion of fruit set in a spike in the varieties was approximately six to seven weeks. Hundred berry fresh weight, volume and dry weight were significantly higher in Panniyur 1. The fresh weight and volume of berries increased up to 165 days in Karimunda and 180 days in Panniyur 1. About 75 per cent of the fresh weight and volume were achieved within 90 days after berry set. The growth of berries in volume and fresh weight was exponential till this period and thereafter the growth was steady. The accumulation of dry weight showed a pattern different to that of fresh weight and 15 days more were required to complete dry weight development. The duration from berry set to maturity was 180 days in Karimunda and 195 days in Panniyur 1.

The crop duration from flowering to berry maturity was approximately 210 to 225 days. The extension growth of lateral during a season was completed within 13 to 14 weeks. The rate of growth was more in Karimunda. More than 90 per cent of the growth was completed within 9 to 10 weeks. The growth was exponential till 7th week and thereafter the growth was steady and gradually declined.

6.2 Characters of lateral at berry maturity

The leaf production in the laterals was significantly higher in Karimunda. However, the average leaf area and leaf area of the lateral was significantly higher in Panniyur 1. Leaf production and leaf area showed an increasing trend from lower to upper canopy level in Panniyur 1, while a reverse trend was observed in Karimunda.

The current season length of laterals was significantly higher in Karimunda in all the canopy levels. While the number of nodes was more in Karimunda, the internodal length was higher in Panniyur 1. There was an increasing trend in internodal length towards upper canopy levels in Panniyur 1.

The spike production per lateral also was significantly more in Karimunda at all canopy levels. The spike production increased with increasing canopy levels in both the varieties.

6.3 Fresh weight and dry weight accumulation and partitioning in the laterals

The stem fresh weight and dry weight, leaf fresh weight, spike fresh weight and dry weight and total fresh weight and dry weight of laterals were significantly higher in Panniyur 1. The upper canopy level registered significantly higher fresh weight of stem in Panniyur 1. Leaf fresh weight showed a decreasing trend towards upper canopy levels. Spike fresh weight and dry weight were higher in the upper canopy levels in both the varieties. There was no canopy level variation in the accumulation of total fresh weight of lateral in Karimunda. However, in the variety Panniyur 1, the upper canopy level recorded maximum fresh weight of lateral.

In the laterals of variety Karimunda, maximum biomass was partitioned to leaves. Where as in Panniyur 1, maximum biomass was partitioned to spikes. Partitioning of fresh and dry weight was in the decreasing order of spike, leaf and stem in Panniyur 1, while this was in the order of leaf, spike and stem in

Karimunda. The percentage partitioning of fresh weight and dry weight in leaf and stem were significantly higher in Karimunda, while the fresh weight and dry weight partitioned to spikes were higher in Panniyur 1. The lower canopy recorded maximum partitioning of fresh weight and dry weight to leaf. There was no canopy level variation in partitioning of fresh weight and dry weight to the stem. Dry weight partitioning by spikes was the highest in upper canopy levels.

6.4 Spike and yield characters

Spike length, 100 berry weight and volume, number of developed berries and total number of berries per spike were significantly higher in Panniyur 1 compared to Karimunda. The upper canopy recorded significantly higher berry weight and volume and total berries per spike. The number of spikes was significantly higher in Karimunda. However, average spike weight and green and dry pepper yield were significantly higher in Panniyur 1. Number of spikes, spike and berry fresh weight and dry pepper yield were higher in the upper canopy level.

6.5 Physiological parameters

Specific leaf area, specific gravity of berries and specific leaf weight did not vary between varieties. However, leaf weight ratio and spike to leaf ratio were high in Karimunda

6.6 Photosynthetic parameters

The average leaf photosynthetic rate was higher (2.001 μmol $m^{-2}s^{-1}$) in Panniyur 1. The photosynthetic rate increased towards upper canopy levels. The periods of flushing and flowering were coincided with maximum photosynthetic rate. Spike bearing laterals recorded significantly higher photosynthetic rate during all stages.

Stomatal conductance (g_s) also showed a pattern similar to photosynthetic rate. The variety Panniyur 1 recorded higher average leaf stomatal conductance.

The leaves of the upper canopy had significantly higher stomatal conductance. This showed a declining trend in the latter part of the season in both the varieties.

The sub-stomatal CO_2 level (Ci) in the leaves was significantly higher in Karimunda. The upper canopy levels recorded higher Ci and the laterals with spike had more Ci compared to laterals without spikes. There was a decreasing trend in Ci in the leaves from flowering to maturity. The carboxylation ratio (A/Ci) was more for Panniyur 1 indicating higher photosynthetic efficiency.

Stomatal resistance (r_s) was higher in Karimunda compared to Panniyur 1. The lower canopy recorded the highest r_s in Karimunda. The r_s values were highly fluctuating and showed a declining trend towards berry maturity.

The transpiration rate of leaves was significantly higher in Panniyur 1 compared to Karimunda irrespective of canopy level and stage of growth. This was found higher in the upper part of canopy.

The leaf surface temperature also was significantly higher in Panniyur 1 compared to Karimunda. The upper canopy levels recorded more leaf temperature especially in Panniyur 1. There was a gradual increase in leaf temperature as the season advanced from flowering to harvest.

The PAR received at leaf surface by Panniyur 1 was significantly higher at all canopy level. The top canopy level received maximum PAR and spike bearing laterals had more PAR compared to those without spike.

The vapour pressure deficit (VPD) was significantly higher in the leaves of Panniyur 1. Middle canopy level had recorded the lowest VPD and was highest in the upper canopy. VPD was highly fluctuating between the growth stages observed.

6.7 Biochemical parameters

The chlorophyll development during leaf area increase followed similar patterns in both Karimunda and Panniyur 1. Total chlorophyll content was significantly higher in Panniyur 1 compared to Karimunda up to 27 days of opening of leaf. However on 35th day, there was not much variation in chlorophyll content between varieties.

During the developmental stages, average chlorophyll 'a' and total chlorophyll content were significantly higher in Karimunda. Chlorophyll 'b' content did not differ between varieties. Leaves from the middle canopy level had recorded higher chlorophyll content and spike bearing laterals recorded higher chlorophyll content than those without spikes. There was no definite trend in the chlorophyll production in leaves during the different stages of development of lateral.

The carbohydrate content of leaves was significantly higher in Panniyur 1 compared to Karimunda. The carbohydrate content was fluctuating between stages. Highest value was recorded during berry maturity stage. The accumulation of carbohydrates was higher in the lower canopy in Panniyur 1. Leaves from spike bearing laterals had significantly more content of carbohydrate compared to laterals without spike.

The phenol content of leaves was significantly high in Karimunda. The upper canopy recorded higher phenol content. Leaves from the laterals with spike had significantly high content of phenols. The phenol content did not vary significantly between growth stages in the varieties except during berry maturity.

There was no variation in the amino acid content between varieties. The canopy level variation in amino acid content was significant only in Karimunda with the middle and upper canopy recording higher values. The amino acid content of leaves was highest during flushing and flowering. Spike bearing laterals had significantly higher content of amino acids.

The electrophoretic pattern of berry proteins showed variation between varieties. In Karimunda, six bands were seen whereas in Panniyur 1 eight bands were seen. The banding pattern among replications did not show intra-varietal differences in Panniyur 1.

6.8 Studies on partitioning of labelled photosynthates

The pattern of partitioning of labelled photosynthates among the components of the laterals showed varietal variations. At flushing stage, most of the activity of labelled CO_2 could be traced from the fed leaf itself in both the varieties. At flowering stage, the variety Karimunda retained maximum activity in the source leaf itself while the spikes partitioned maximum labelled CO_2 in Panniyur 1. At berry set stage also, leaves partitioned the maximum photo assimilates in Karimunda. However, the spikes shared the maximum of the radioactivity fixed by the plants in Panniyur 1. At berry development stage, the stem of the lateral recorded maximum radioactivity in the variety Karimunda. In Panniyur 1, at this stage also, spikes commanded the maximum share of labelled photosynthates.

The translocation of labelled photosynthates to the spikes increased up to third day after feeding in Karimunda at berry set and berry development stage. In Panniyur 1, maximum activity was traced at 24 hours after feeding at berry set stage and up to third day during berry development stage.

6.9 Correlation studies

Morphological traits, gas exchange parameters and biochemical characters were correlated with yield and their interrelationships were assessed. The characters of the lateral that exhibited significant positive association with yield were total fresh weight and dry weight of the lateral, fresh weight and dry weight of stem and fresh weight of leaf. Leaf area showed significant correlation with fresh weight and dry weight of spike and stem, and total dry weight of the lateral. Among the characters of spikes and berries, number of developed berries and total berries, and spike length recorded significant association with yield. Characters of the plant such as fresh weight of berries and spike, number of spikes and dry weight percentage of berries also showed high correlation with economic yield.

Among the gas exchange parameters, only leaf photosynthetic rate registered significant correlation with yield. Stomatal resistance, transpiration rate, vapour pressure deficit and sub-stomatal CO_2 concentration exhibited negative correlation with yield.

Among the biochemical characters, chlorophyll and carbohydrate content of leaves showed significant correlation with yield at five per cent level.

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* Originals not seen

Appendices

Appendix: 1
Rain fall (mm) data at P.R.S. Panniyur

Sl.No.	Year	1997		1998	
	Month	**Rain fall**	**Rainy days**	**Rain fall**	**Rainy days**
1	January	0.0	0	0.0	0
2	February	0.0	0	0.0	0
3	March	3.0	1	0.0	0
4	April	2.8	1	10.0	1
5	May	64.2	7	124.8	9
6	June	1153.6	21	990.6	26
7	July	1613.6	31	1106.5	28
8	August	781.7	22	298.0	21
9	September	142.2	11	535.2	18
10	October	113.5	11	349.5	17
11	November	293.4	12	88.1	8
12	December	91.2	6	91.0	3

Appendix : II
Inter correlation matrix of morphological characters and yield in black pepper

Characters*	*1*	*2*	*3*	*4*	*5*	*6*	*7*	*8*	*9*	*10*	*11*	*12*	*13*	*14*	*15*	*16*	*17*	*18*	*19*	*20*	*21*	*22*
1	1																					
2	0.002	1																				
3	0.123	0.209	1																			
4	0.334	-0.562	0.079	1																		
5	0.298	-0.609	0.050	0.765	1																	
6	0.092	0.719	0.299	-0.352	-0.349	1																
7	-0.044	0.826	0.238	-0.529	-0.557	0.741	1															
8	0.267	-0.178	0.331	0.273	0.324	0.120	-0.134	1														
9	0.255	0.086	0.710	0.234	0.207	0.263	0.112	0.541	1													
10	0.426	-0.341	0.401	0.600	0.551	-0.084	-0.352	0.653	0.649	1												
11	0.177	-0.079	0.265	0.177	0.212	0.198	-0.045	0.966	0.449	0.554	1											
12	0.166	0.250	0.689	0.025	0.056	0.382	0.290	0.511	0.871	0.483	0.479	1										
13	0.445	-0.341	0.377	0.488	0.493	-0.060	-0.297	0.683	0.607	0.906	0.590	0.505	1									
14	0.339	-0.075	-0.088	0.039	0.074	-0.012	-0.072	0.060	-0.132	0.031	0.047	-0.156	0.084	1								
15	0.439	-0.458	0.187	0.573	0.621	-0.339	-0.510	0.502	0.323	0.681	0.394	0.158	0.672	0.108	1							
16	0.382	-0.593	0.166	0.662	0.742	-0.403	-0.546	0.357	0.263	0.623	0.226	0.062	0.617	0.060	0.756	1						
17	0.474	-0.452	0.229	0.596	0.671	-0.273	-0.473	0.477	0.372	0.690	0.339	0.180	0.710	0.103	0.823	0.811	1					
18	0.017	0.015	0.052	-0.128	-0.009	0.069	0.026	0.341	0.093	0.110	0.392	0.165	0.146	0.086	0.213	-0.008	0.013	1				
19	0.457	-0.477	0.231	0.579	0.667	-0.301	-0.530	0.522	0.386	0.718	0.394	0.202	0.744	0.132	0.861	0.834	0.949	0.149	1			
20	0.541	0.570	-0.033	-0.372	-0.433	0.433	0.514	-0.070	-0.033	-0.227	-0.031	0.074	-0.177	0.161	-0.227	-0.371	-0.238	0.010	-0.274	1		
21	0.935	0.005	0.070	0.292	0.268	0.083	-0.063	0.258	0.224	0.362	0.179	0.140	0.373	0.283	0.401	0.353	0.442	0.004	0.423	0.586	1	
22	0.987	0.008	0.137	0.328	0.283	0.089	-0.047	0.267	0.281	0.436	0.176	0.184	0.450	0.265	0.450	0.386	0.483	0.021	0.4664	0.554	0.939	1

Characters* 1. Dry pepper yield 2. Number of leaves 3. Leaf area per lateral 4. Hundred berry weight 5. Hundred berry volume 6. Length of lateral 7. Number of nodes 8. Fresh weight of stem 9. Fresh weight of leaf 10. Total fresh weight of lateral 11. Dry weight of stem 12. Dry weight of leaf 13. Total dry weight of lateral 14. Dry weight percentage of berry 15. Length of spike 16. Average spike weight 17. Number of developed berries 18. Number of undeveloped berries 19. Total number of berries per spike 20. Number of spikes per plant 21. Fresh weight of spikes 22. Fresh weight of berries

Appendix : III

Inter correlation matrix of gas exchange parameters and yield in black pepper

Characters*	1	2	3	4	5	6	7	8	9
1	1								
2	0.195	1							
3	-0.018	0.068	1						
4	-0.018	0.068	1	1					
5	-0.026	0.116	-0.361	-0.361	1				
6	0.026	-0.216	-0.345	-0.345	0.369	1			
7	0.050	0.454	-0.133	-0.133	0.247	0.380	1		
8	-0.048	0.074	-0.268	-0.268	0.584	0.388	0.227	1	
9	-0.001	0.563	0.077	0.077	0.122	-0.146	0.397	0.075	1

Characters* 1. Dry pepper yield 2. Photosynthetic rate 3. Stomatal resistance 4. Stomatal conductance 5. Transpiration rate 6. Leaf surface temperature 7. Photosynthetically active radiation 8.Vapour pressure deficit 9. Internal CO_2 concentration

Appendix : IV

Inter correlation matrix of biochemical characters and yield in black pepper

Characters*	1	2	3	4	5	6	7
1	1						
2	0.093	1					
3	0.113	0.890	1				
4	0.108	0.955	0.985	1			
5	0.089	-0.008	-0.021	-0.016	1		
6	0.059	-0.047	-0.034	-0.040	0.238	1	
7	0.052	0.143	0.148	0.150	0.022	-0.231	1

Characters* 1. Dry pepper yield 2. Chlorophyll 'a' 3. Chlorophyll 'b' 4. Total chlorophyll 5. Carbohydrate 6. Phenolics 7. Amino acid

Abstract

PHYSIOLOGICAL AND BIOCHEMICAL ASPECTS OF FLOWERING, BERRY SET AND DEVELOPMENT IN BLACK PEPPER (*Piper nigrum* L.)

By

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ABSTRACT OF THE THESIS

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ABSTRACT

Black pepper (*Piper nigrum* L.) is an important cash crop of Kerala and contributes significantly to the agrarian economy of the State. In spite of achievements in crop improvement and technological advances in crop management, the productivity of black pepper is consistently low. Hence an experiment entitled 'Physiological and biochemical aspects of flowering, berry set and development in black pepper (*Piper nigrum* L.)' was conducted at Pepper Research Station, Panniyur and College of Horticulture, Vellanikkara during 1997 to 1998 to analyse the physiological basis of productivity in this crop. The objectives of the experiment were to trace the chronological events in the growth and development of laterals and to analyse the influence of morphological, physiological, biochemical and photosynthetic parameters on productivity and to elucidate the seasonal pattern in the accumulation of photosynthates in component organs of the laterals. The cultivar Karimunda and a hybrid, Panniyur 1, were selected for the study.

Flushing of the vines commenced within a week after continuous rains during the monsoon in June and the variety Panniyur 1 was earlier to flush. The leaf area development completed in about 35 days in both the varieties. Fresh and dry weights of leaf increased till 50 days after flushing and thereafter these parameters registered wide fluctuation up to berry maturity. Leaf production was more in Karimunda and upper canopy levels produced more leaves. The plastochron index was 23 days on an average in both the varieties.

There was synchronous flushing and flowering and the emergence of spike was delayed up to 6-9 days after flushing among the varieties. Spike growth was completed within 35-42 days after emergence. The fresh weight of spikes increased up to 150 days after berry set. The number of spikes produced per lateral and per vine was significantly higher in Karimunda and spike production was more in the upper canopy levels.

The fresh weight and volume of berries increased up to 165 to 180 days after berry set and increase in dry weight continued for another fortnight. The extension growth of laterals ceased after a period of 13 to 14 weeks.

The leaf and spike productions in the laterals were more in Karimunda and the leaf area was more in Panniyur 1. The leaf production, leaf area and spike production increased towards upper canopy levels.

The total fresh weight and dry weight of the lateral during a season was more in Panniyur 1 and was higher in the upper canopy levels. Biomass partitioning to the spikes at berry maturity period also showed superiority of Panniyur 1. Partitioning of fresh weight and dry weight was in the decreasing order of spike, leaf and stem in Panniyur 1, while this was in the order of leaf, spike and stem in Karimunda. The partitioning of fresh weight and dry weight to spikes were also more in the upper canopy levels.

Spike length, berry size, number of developed berries and total number of berries per spike, average spike weight and green and dry pepper yield was more in Panniyur 1. However, more number of spikes per lateral and per vine were observed in Karimunda.

Specific leaf weight and spike to leaf ratio were higher in Karimunda and leaf area duration was more in Panniyur 1. The variety Panniyur 1 recorded a higher average leaf photosynthetic rate compared to Karimunda. Maximum photosynthetic rate coincided with flushing and flowering, and the spike bearing laterals recorded higher photosynthetic rate.

Stomatal conductance, leaf surface temperature, transpiration, vapour pressure deficit and PAR at leaf surface recorded by the leaves are more in Panniyur 1. The sub-stomatal CO_2 level and stomatal resistance of leaves were higher in Karimunda. The leaves of the upper canopy recorded higher stomatal conductance, sub stomatal CO_2 level, transpiration rate, leaf surface temperature, PAR and VPD. The stomatal conductance, sub stomatal CO_2 and stomatal resistance declined gradually towards berry maturity. Transpiration rate, leaf surface temperature and VPD increased towards berry maturity.

Chlorophyll development was completed in 35 days after flushing and chlorophyll 'a' and total chlorophyll content of leaves were higher in Karimunda. Middle canopy recorded more chlorophyll content and spike bearing laterals had higher chlorophyll content of leaves.

Carbohydrate content was more in the leaves of Panniyur 1 while the phenolic content was higher in Karimunda. There was no significant difference in the amino acid content between varieties. Carbohydrate accumulation was more in the lower canopy while the upper canopy levels recorded higher phenolic and amino acid contents. The carbohydrate and amino acid contents of leaves fluctuated with the season while the phenolic content of leaves was almost stable except at berry maturity. The spike bearing laterals recorded more foliar carbohydrates, phenols and amino acids.

The electrpophoretic pattern of proteins in the berries showed variation between varieties. The number of bands seen was six and eight respectively for Karimunda and Panniyur 1.

The pattern of partitioning of labelled photosynthates among component organs showed that in Karimunda, maximum amount of photosynthates were fixed by the fed leaf itself during flushing, flowering and berry set. In Panniyur 1, except at flushing stage, the berries partitioned the maximum labelled photosynthates. During all the stages, the percentage of labelled photosynthates partitioned by the spikes was higher in Panniyur 1 compared to Karimunda.

Fresh weight and dry weight of the lateral, fresh weight and dry weight of spikes, number of developed berries in a spike, spike length and number of spikes showed significant correlation with dry pepper yield. Leaf photosynthetic rate, chlorophyll and carbohydrate content of leaves also were significantly associated with economic yield in black pepper.