

## Effect of fruit growth, temperature and irradiance on biomass allocation to the vegetative parts of cucumber

L.F.M. MARCELIS

DLO Research Institute for Agrobiological and Soil Fertility (AB-DLO), P.O. Box 14,  
NL-6700 AA Wageningen, The Netherlands

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### Abstract

Cucumber plants were grown at 18 or 25°C with four intensities of fruit removal or at three different levels of irradiance in order to analyse the effects of fruit growth, temperature and irradiance on the dry matter allocation to leaves, stems, petioles and roots. With increasing irradiance the dry weight of the vegetative part of the shoot increased, but the proportion of the total dry matter distributed to this part decreased. An increase in irradiance enhanced stem dry matter production less than leaf and petiole dry matter production which was in turn less stimulated than root dry matter production. In fruit bearing plants an increase in temperature had no effect on the dry matter allocation to the leaves, stems and petioles, but reduced the allocation to the roots. Fruit growth strongly reduced dry matter production of all vegetative plant parts, but the distribution between stems, leaves and petioles was only slightly affected. At 25°C the dry matter distribution between the roots and the vegetative part of the shoot was not affected by fruit growth but at 18°C the weight ratio of root to vegetative shoot part decreased with increasing number of fruits on the plant.

The biomass allocation between roots and shoot is discussed in relation to the functional equilibrium concept.

**Keywords:** cucumber, *Cucumis sativus* L., dry matter distribution, fruit load, functional equilibrium, irradiance, light, partitioning, root-shoot ratio, temperature, vegetative-generative growth

### Introduction

The root-shoot ratio is often believed to be determined by a functional equilibrium between the activities of the shoot and the root (Brouwer, 1963). The main activities of the root are water and nutrient uptake while the main activity of the shoot is photosynthesis. Constant ratios between the weights of root and shoot have often been interpreted as being the result of a functional equilibrium (Brouwer, 1962; Hurd et al., 1979; Nielsen & Veierskov, 1988). Once a plant enters the reproductive stage, it is not clear whether the total shoot or only the vegetative part of the shoot is involved in the functional equilibrium (Hurd et al., 1979; Nielsen & Veierskov, 1988).

Most information on biomass allocation among vegetative organs has been obtained from experiments with young vegetative plants. The number of experiments with fruiting plants is limited. Although it is well known that fruit growth reduces the vegetative growth rate of plants (Wardlaw, 1990), the experimental results about the effects of fruit growth on the biomass allocation among the vegetative organs are contradictory (Claussen, 1976; Heim et al., 1979; Hurd et al., 1979; Pharr et al., 1985; Nielsen & Veierskov, 1988).

In fruiting cucumber plants the dry matter distribution among individual fruits and between the fruits and the rest of the plant strongly depends on fruit load, temperature and irradiance (Marcelis, 1993a, b). However, their effects on the biomass allocation among the vegetative organs (stems, leaves, petioles and roots) have not been examined. In this paper the effects of fruit growth, temperature and irradiance on the dry matter allocation to leaves, stems, petioles and roots in cucumber are analysed.

## Materials and methods

In all experiments seeds of cucumber (*Cucumis sativus* L. cv. Corona) were germinated in moist perlite in the dark at 30°C. After three days, seedlings were transferred to an aerated modified Hoagland solution (Steiner, 1984) in an air-conditioned glasshouse. Leaves were removed when they were entirely shaded by adjacent leaves or when they started yellowing (5-7% of the final leaf dry weight was removed before the end of the experiments). A fruit was harvested when its estimated fresh weight exceeded 350-400 g (Experiment 1) or 400-450 g (Experiment 2) or when its fresh weight increase was estimated to be less than 0.1 g in three days for fruits younger than 10 days, or less than 10 g in three days for fruits older than 10 days. The fresh weight of the fruits was estimated from measurements of length and circumference, as described elsewhere (Marcelis, 1992).

At the end of the experiments cumulative leaf area and cumulative dry weights (after drying at 100°C for 48 h) of the roots, stems, leaves, petioles and fruits were determined, including all plant parts removed previously. The data were analysed by analysis of variance and least significant differences were calculated according to Student's t-test.

Temperature, CO<sub>2</sub> concentration and total solar radiation inside the glasshouse (above the canopy) were measured every minute by a shielded PT-100 sensor, an infra-red gas analyser (BINOS, Leybold-Heraeus) and a thermopile (Kipp and Zonen), respectively. The air humidity was measured by a thermohygrometer.

### *Experiment 1: Effects of irradiance on biomass allocation*

Seeds were sown on 25 June 1990. From 18 days after sowing, plants were grown at three different levels of irradiance by shading the plants over the tops and along the sides with none, a single or a double layer of cheese cloth (transmittance 100, 50 and 30%, respectively).



The main stem of the plants was topped at a height of approximately 1.75 m. All but the two uppermost side shoots of the main stem were removed. Branching of the side shoots was not restricted. In accordance with commercial practice forty per cent of the flowers on the main stem were allowed to remain on the plant. The number of fruits on the side stems was not restricted manually.

The treatments were arranged in a randomized block design. The experiment was carried out in four identical glasshouse compartments. In each compartment plants were grown in three rows of three plants. The same level of shading was applied to all three plants in a row. The plants in one glasshouse compartment were harvested 31 days after sowing. The plants in the other three compartments, representing three blocks, were harvested 80 days after sowing.

The average temperature was 24.5°C (24.7/24.2°C day/night). Measurements by thermocouples indicated that shading affected the temperature less than 0.5°C. The average total solar radiation inside the glasshouse was 4.94 MJ m<sup>-2</sup> d<sup>-1</sup> for the unshaded plants, the average relative air humidity was 75% and during day time the average CO<sub>2</sub> concentration was 403 vpm.

#### *Experiment 2: Effects of number of fruits and temperature on biomass allocation*

The experiment was repeated in two consecutive periods. Seeds were sown on 28 March 1989 and 14 July 1989. From 14 days after sowing, plants were grown at 18 or 25°C. Four intensities of fruit removal were maintained: one fruit left per leaf axil, one fruit left per three leaf axils, one fruit left per six leaf axils, or all fruits removed. The fruit number was imposed by removing the ovaries daily. In all treatments no fruits were allowed to grow in the five lowermost leaf axils. The main stem of the plants was topped at a height of approximately 1.75 m. All but the two uppermost side shoots of the main stem were removed. The side shoots of the two shoots retained were also removed.

The treatments were arranged in a split-plot design with temperature at the whole-plot level and number of fruits at the sub-plot level. For plants of the first sowing date the low and the high temperature were randomized over two identical glasshouse compartments. For plants of the second sowing date the assignment of the low and high temperature to the compartments was changed. In each compartment plants were grown in three rows of four plants. Each row represented a block. Per block each plant had another sub-plot treatment (number of fruits). All plants of one temperature treatment were harvested at the same time when they had produced on average about 60 leaves (95 days after sowing at 18°C and 68 days at 25°C).

At the 18 and 25°C temperature treatments the actual average temperature was 17.5 (19.2/14.6°C day/night) and 24.6°C (26.2/21.7°C day/night), respectively; the average total solar radiation inside the glasshouse was 5.70 and 6.11 MJ m<sup>-2</sup> d<sup>-1</sup>, respectively; during day time the average CO<sub>2</sub> concentration was 382 and 388 vpm, respectively, and in both treatments the average relative air humidity was 75%.

## Results and discussion

### *Allocation to the vegetative parts of the shoot*

The dry matter allocation to the vegetative part of the shoot (the ratio of the vegetative shoot part to total plant weight) decreased with increasing irradiance (Table 1). However, the absolute dry weight of this vegetative part increased because of an increase in total plant dry matter production. Among the vegetative parts of the shoot the dry matter distribution to the stems decreased with increasing irradiance in favour of leaves and petioles (Table 1). Harssema (1977) and Nilwik (1981) observed also an increase in the ratio of leaf to plant weight at high irradiance levels in young tomato and sweet pepper plants, which is a general response of shade avoiding plants to irradiance (Smith, 1981). However, Horie et al. (1979) found no appreciable effects of irradiance on the dry matter distribution between leaves and stem of young cucumber plants.

From 31 days after sowing the dry matter distribution among leaves, petioles and stems remained almost constant with time as indicated by a comparison between the data of the final harvest at 80 days after sowing (Table 1) and the data of plants harvested 31 days after sowing. At 31 days after sowing total plant dry weight was 7 g per plant and the relative weights of stem:leaf:petiole were 30:58:11 at the 30% irradiance level; at the 100% irradiance level the equivalent figures were 25 g per plant and 22:64:14 (data are means of 3 replicate plants). In accordance with our results Schapendonk and Brouwer (1984) observed that the ratio between the weights of leaf and stem of fruiting cucumber plants was almost constant with time. In contrast to older plants, in young cucumber plants the leaf to stem weight ratio (after an initial increase) decreases with plant size (Horie et al., 1979).

As long as some fruits were present on the plant, the dry matter allocation to the vegetative part of the shoot (the ratio of the vegetative shoot part to total plant weight) was not affected by temperature (Table 2). However, when all fruits were removed, the dry matter distribution to the vegetative part of the shoot was greater at

Table 1. Effects of irradiance on the dry weights of the total plant<sup>a</sup> and the vegetative shoot part<sup>b</sup>, the ratio of vegetative shoot part to total plant dry weight and the ratios of stem, leaf and petiole to dry weight of the vegetative shoot part. Plants were harvested 80 days after sowing. Data are means of 9 replicate plants (Experiment 1).

Irradiance <sup>c</sup> (%)	Total plant (g plant <sup>-1</sup> )	Shoot (g plant <sup>-1</sup> )	Shoot/plant (g g <sup>-1</sup> )	Stem/shoot (g g <sup>-1</sup> )	Leaf/shoot (g g <sup>-1</sup> )	Petiole/shoot (g g <sup>-1</sup> )
30	79	45	0.58	0.31	0.56	0.12
50	160	80	0.50	0.26	0.58	0.15
100	408	169	0.42	0.22	0.62	0.17
LSD (P = 0.05)	40	19	0.10	0.02	0.02	0.01

<sup>a</sup> Total plant represents stems + leaves + petioles + roots + fruits

<sup>b</sup> Vegetative shoot part represents stems + leaves + petioles

<sup>c</sup> 100% = 4.94 MJ m<sup>-2</sup> d<sup>-1</sup> total solar radiation inside glasshouse



25 than at 18°C. The dry matter distribution among the vegetative parts of the shoot (stems, petioles and leaves) was not affected by temperature (Table 2) which is in accordance with data on dry matter distribution between stem and leaves in fruiting sweet pepper plants (Bhatt & Srinivasa Rao, 1989). In young vegetative plants the dry matter distribution to the leaves is often insensitive to temperature (Warren Wilson, 1966; Harssema, 1977). However, Nilwik (1981) and Kleinendorst & Veen (1983) reported for respectively young sweet pepper and young cucumber plants that with increasing temperature the dry matter distribution to the leaves decreased in favour of the stem. The effects reported by Kleinendorst & Veen (1983) should probably at least partly be ascribed to ontogenetic effects because the leaf to stem weight ratio changes with plant size in young cucumber plants, as discussed before.

Although the dry matter production of the vegetative parts of the shoot strongly diminished with increasing number of fruits per plant, the dry matter allocation between stems, leaves and petioles was only slightly affected (Table 2). With increasing number of fruits, the weight ratio of leaf to vegetative shoot part increased slightly at the expense of the weight ratio of petiole to vegetative shoot part and at 25°C also at the expense of the weight ratio of stem to vegetative shoot part (Table 2). In pepper and apple, the ratio of leaf to stem weight also increased with increasing fruit growth (Hall, 1977; Heim et al., 1979; Nielsen & Veierskov, 1988). As we measured only a very small effect of fruit growth on the weight ratio between leaves,

Table 2. Effects of temperature and number of fruits retained on the dry weights of the total plant<sup>a</sup> and the vegetative shoot part<sup>b</sup>, the ratio of vegetative shoot part to total plant dry weight and the ratios of stem, leaf and petiole to dry weight of the vegetative shoot part. All plants of one temperature treatment were harvested when they had on average about 60 leaves. Data are means of 6 replicate plants (Experiment 2).

Temperature (°C)	No. of fruits retained <sup>c</sup>	Total plant (g plant <sup>-1</sup> )	Shoot (g plant <sup>-1</sup> )	Shoot/plant (g g <sup>-1</sup> )	Stem/shoot (g g <sup>-1</sup> )	Leaf/shoot (g g <sup>-1</sup> )	Petiole/shoot (g g <sup>-1</sup> )
18	0/0	301	248	0.82	0.21	0.60	0.19
	1/6	314	199	0.63	0.21	0.61	0.18
	1/3	376	200	0.52	0.22	0.61	0.17
	1/1	340	148	0.45	0.21	0.62	0.17
	Mean	333	199	0.61	0.21	0.61	0.18
25	0/0	257	241	0.94	0.24	0.57	0.19
	1/6	234	142	0.61	0.23	0.60	0.17
	1/3	229	117	0.51	0.23	0.61	0.17
	1/1	216	98	0.45	0.21	0.63	0.16
	Mean	234	150	0.63	0.23	0.60	0.17
LSD (P = 0.05) <sup>d</sup>		133	81	0.03	0.03	0.03	0.01

<sup>a</sup> Total plant represents stems + leaves + petioles + roots + fruits

<sup>b</sup> Vegetative shoot part represents stems + leaves + petioles

<sup>c</sup> x/y: x fruits per y leaves

<sup>d</sup> LSD: Least significant differences between treatment combinations of temperature and fruit number

stems and petioles, in cucumber the fruits seem to compete with the vegetative part of the shoot (stems, leaves and petioles) almost as an entity.

#### *Allocation to the roots*

Dry weight of the roots was relatively more stimulated by high irradiance than that of the vegetative shoot part (Tables 1 and 3). The ratio of root dry weight to total plant dry weight increased slightly with increasing irradiance. The weight of the roots per leaf area also increased with increasing irradiance.

An increase in the dry matter distribution to the roots with increasing irradiance has been observed in many plant species (Brouwer, 1962). This phenomenon has often been explained by a functional equilibrium. With increasing irradiance the specific activity (activity divided by weight) of the shoot increases while the specific root activity remains constant. As a consequence, when the ratio between the total activities of the shoot and the roots has to remain constant, the ratio of shoot to root weight has to decrease.

Like the distribution among leaves, petioles and stems, the distribution between roots and vegetative part of the shoot remained constant with time (from 31 until 80 days after sowing): 31 days after sowing the ratio between the weight of roots and all vegetative plant parts was 0.047 and 0.077 at the 30 and 100% irradiance level, respectively (data are means of 3 replicate plants); which values are close to those given in Table 3. This observation that the dry matter distribution among the vegetative organs is more or less constant with time in older cucumber plants corroborates the data of Schapendonk & Brouwer (1984).

At 25°C the dry matter allocation to the roots (the ratio of root to total plant weight) was much lower than at 18°C (Table 4). Consequently, when all fruits were removed, the dry matter distribution to the vegetative part of the shoot increased with increasing temperature (Table 2). In fruit bearing plants the decrease in the dry matter distribution to the roots was not accompanied by an increase in the distribution to the vegetative part of the shoot (Table 2), but the distribution to the fruits increased with increasing temperature (Marcelis, 1993a). When the number of fruits

Table 3. Effects of irradiance on the dry weight of the roots, the ratios of root dry weight to total plant dry weight<sup>a</sup>, to total dry weight of the vegetative parts<sup>b</sup> and to leaf area. Plants were harvested 80 days after sowing. Data are means of 9 replicate plants (Experiment 1).

Irradiance <sup>c</sup> (%)	Roots (g plant <sup>-1</sup> )	Root/plant (g g <sup>-1</sup> )	Root/vegetative parts (g g <sup>-1</sup> )	Root/leaf area (g m <sup>-2</sup> )
30	2.0	0.026	0.044	1.5
50	4.3	0.027	0.052	2.1
100	13.7	0.034	0.075	4.0
LSD (P = 0.05)	2.2	0.006	0.012	0.8

<sup>a</sup> Total plant represents stems + leaves + petioles + roots + fruits

<sup>b</sup> Vegetative parts represent stems + leaves + petioles + roots

<sup>c</sup> 100% = 4.94 MJ m<sup>-2</sup> d<sup>-1</sup> total solar radiation inside glasshouse



# BIOMASS ALLOCATION IN CUCUMBER

Table 4. Effects of temperature and number of fruits retained on the dry weight of the roots, the ratios of root dry weight to total plant dry weight<sup>a</sup>, to total dry weight of the vegetative parts<sup>b</sup> and to leaf area. All plants of one temperature treatment were harvested when they had on average about 60 leaves. Data are means of 6 replicate plants (Experiment 2).

Temperature (°C)	No. of fruits retained <sup>c</sup>	Roots (g plant <sup>-1</sup> )	Root/plant (g g <sup>-1</sup> )	Root/vegetative parts (g g <sup>-1</sup> )	Root/leaf area (g m <sup>-2</sup> )
18	0/0	53.3	0.180	0.180	12.3
	1/6	37.3	0.122	0.162	9.7
	1/3	38.2	0.100	0.161	10.1
	1/1	23.5	0.071	0.139	7.6
	Mean	38.1	0.118	0.161	9.9
25	0/0	16.3	0.062	0.062	3.2
	1/6	9.4	0.039	0.060	2.7
	1/3	7.9	0.034	0.063	2.6
	1/1	6.6	0.031	0.065	2.7
	Mean	10.0	0.042	0.063	2.8
LSD (P = 0.05) <sup>d</sup>		7.5	0.024	0.027	1.5

<sup>a</sup> Total plant represents stems + leaves + petioles + roots + fruits

<sup>b</sup> Vegetative parts represent stems + leaves + petioles + roots

<sup>c</sup> x/y: x fruits per y leaves

<sup>d</sup> LSD: Least significant differences between treatment combinations of temperature and fruit number

growing at the same time on a plant was kept constant, the dry matter distribution to the vegetative shoot part even decreased with increasing temperature (Marcelis, 1993a).

The ratio between root weight and leaf area was also lower at 25 than at 18°C (Table 4). If there was an equilibrium between the activities of root and shoot, the optimum temperature for the specific rate of root functioning has to be higher than the optimum temperature for the specific rate of shoot functioning. However, from the results it could also be concluded that the optimum temperature for root growth (dry weight accretion of the roots) is lower than the optimum temperature for shoot growth, which agrees with results obtained by Kleinendorst & Veen (1983). Obviously, the optimum temperature for root growth and/or functioning differs from the optimum temperature for shoot growth and/or functioning.

The dry matter distribution to the roots was greatly reduced by an increase in the number of fruits per plant (Table 4). At 18°C the ratio of the root to the total weight of all vegetative plant parts (including roots) decreased with increasing fruit number, but at 25°C this ratio was not affected by the number of fruits.

Fruit growth has been reported to reduce the growth of the roots to a greater extent than growth of other plant organs in several species (Claussen, 1976; Heim et al., 1979; Pharr et al., 1985). However, Hurd et al. (1979) reported for tomato that on the long term fruit growth reduced growth of the roots and the vegetative shoot part to the same extent. In addition, Nielsen & Veierskov (1988) found that a decrease in the weight ratio of root to vegetative shoot part coincided with the onset of fruiting in

pepper, but this ratio decreased to the same extent when all flowers were removed. Our experiments indicate that temperature influences the effects of fruit growth on the biomass distribution between roots and the vegetative part of the shoot. This might explain why the results reported in the literature are contradictory whether or not fruit growth affects the biomass allocation between roots and the vegetative part of the shoot. As the weight of the roots relative to that of the total plant was much smaller at 25°C than at 18°C, at 25°C in contrast to 18°C root growth and/or functioning might have limited plant growth. A constant ratio between the weights of root and shoot may only be expected when the roots are limiting plant growth. This explanation fully agrees with the functional equilibrium concept (Brouwer, 1963). Shoot activity is generally more closely related to leaf area than to shoot weight, but an analysis based on leaf area resulted in the same conclusions as on a weight basis. The fruits might have a function in establishing a functional equilibrium. As the fruits contain a large amount of water, they possibly have a role as a buffer for the relative water content of the plant. Finally it should be concluded that a functional equilibrium theory based on weight ratios cannot explain all our results. Maybe it can only predict a minimum amount of root mass needed for cucumber growing on nutrient solution. In contrast to a low temperature (18°C), at a high temperature (25°C), the actual root mass could be close to the minimum mass needed.

## Conclusions

Fruit load, temperature and irradiance all had a great effect on the biomass allocation to the vegetative plant parts of cucumber. Plants adapted to shade by an increase in the fraction of dry matter distributed to the vegetative parts of the shoot (especially to the stems), while the distribution to the roots decreased. In fruiting plants temperature affected the dry matter distribution to roots but had no great effect on the distribution to the vegetative parts of the shoot. Although fruit growth greatly reduced dry matter production of the stems, petioles and leaves, the fruits seem to compete with the vegetative part of the shoot (stems, petioles and leaves) almost as an entity. The effect of fruit growth on the dry matter distribution between roots and vegetative part of the shoot was dependent on the temperature. Although most of the results on dry matter distribution to the roots could be explained by a functional equilibrium theory based on weight ratios, this theory could not explain all our results. Maybe it can only predict a minimum amount of root mass needed for cucumber growing on nutrient solution.

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