

# The Effect of Light Intensity and Nitrogen Fertilization on Plant Growth and Leaf Quality of Ngo Gai (*Eryngium foetidum* L.) in Massachusetts

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## Abstract

Ngo gai (*Eryngium foetidum* L.) is a leafy green culinary and medicinal herb currently marketed in Massachusetts as an import. The objective of this research was to elucidate the optimal light intensity and nitrogen fertilization rate for the cultivation of ngo gai in Massachusetts. A field trial was implemented in 2001 to examine the growth of transplants under five light regimes (0, 20, 40, 60, and 80 % shade) using shade cloth to reduce incident light. Within each light intensity three rates of nitrogen fertilizer were supplied (0, 45, and 90 kg N/ha) as  $\text{NH}_4\text{NO}_3$  over two applications. Emerging flower stalks were removed on a weekly basis and were weighed and dried.

Sixty days after transplanting, the plants were harvested and biomass production, leaf area, and leaf nitrogen contents were assessed. Plants grown at the highest light intensities produced the greatest numbers of flower stalks, and these were heavier than those produced in the shade. The intermediate nitrogen fertilization level resulted in the greatest flower mass, with the highest fertilization level resulting in the lowest flower mass. Leaf tissue nitrogen content increased with increasing nitrogen fertilization.

Leaf quality increased with increasing shade due to increasing specific leaf area and moisture content of these plants. Plants grown under increasing shade had decreasing biomass production, fewer leaves, and less overall total leaf area. However, the plants grown under increasing shade partitioned more of their biomass to aboveground vegetative production so that the leaf area ratio increased with increasing shade. The highest mean leaf area value was at 40 % shade. Mean leaf area was also affected by rate of nitrogen fertilization resulting in the highest leaf areas at 90 kg N/ha.

Because ngo gai is sold by the bunch rather than by weight, mean leaf area is considered to be the most important parameter to optimize. It was concluded from this research that optimal conditions for ngo gai cultivation in Massachusetts are at 40 % shade with a nitrogen fertilization rate of at least 90 kg N/ha.

## INTRODUCTION

Ngo gai is a leafy green culinary and medicinal herb commonly used throughout the Caribbean islands, Central and South America, and many Asian countries such as India, Vietnam, and Korea. Known as ngo gai in Vietnam, the plant is recognized by several other names: recao and culantro (Puerto Rico and the Dominican Republic), fitweed (Guyana), herbe à fer (Martinique and Guadeloupe), shado beni (Trinidad and Tobago), pak shi farang (Thailand), jia yuan qian (China), and mandhania (India).

The leaves of ngo gai are used mainly as a seasoning in the preparation of many types of food (Mohammed and Wickham, 1994). The nutritional status of leaves from the Assam region in India was studied revealing a high iron content (Saika and Shadeque, 1993). Ngo gai has long been used in folk medicine (Wong, 1976) and recently anti-convulsant and anti-inflammatory properties of leaf extracts were confirmed (Simon and Singh, 1986; Saenz et al., 1997). Ngo gai is widely cultivated in such places as Trinidad and Tobago, Costa Rica and Puerto Rico for local consumption and for export to the United States and other countries. In 1988, Puerto Rico exported 165,000 kg of ngo gai to

the United States at a value of \$201,000 (Ramcharan, 1999).

The population in Massachusetts is comprised of increasing numbers of people of Latin American and Asian descent. Not surprisingly, a concomitant increase in demand for foods common in the respective cuisines of these ethnic groups is occurring. Presently all the ngo gai marketed in Massachusetts is imported. However, because it is a leafy green herb it has a limited postharvest life (Mohammed 1992; Sankat and Maharaj, 1996). Therefore, it is desirable for consumers and growers to have a local source of this herb.

The literature presents some conflicting information regarding the habitat of ngo gai, stating that it is found in sunny or shaded areas (Dassanayake and Fosberg, 1981), in moist fields (Morton, 1981), and on well-drained open fields (Banjeree and Pal, 1984). Since no accession numbers have been assigned to this plant it is difficult to evaluate the nature and cause of such an apparent diverse habitat range.

Ngo gai produces abundant flower stalks which, if allowed to develop, limit the yield of the leaves (Ramcharan, 1999). However, an added labor cost is involved in removing the flower stalks, so efforts have been made to prevent floral initiation and development. It is possible to suppress flowering in some plants by reducing the light level to which they are subjected (Armitage and Wetzstein, 1984; Nell et al., 1981; Neumaier and Blessington, 1987). Santiago-Santos and Cedeno-Maldonado (1991) determined that flowering was significantly suppressed at 63 % and 73 % shade. In addition, the leaves developed at these light levels were greener, longer, and heavier than those developed under ambient light. Large and thin leaves tend to develop in reduced light levels as part of a shade-tolerant response in plants (Corre, 1983). Because the market prefers large leaves of ngo gai, its commercial cultivation is frequently conducted under shade cloth (Santiago-Santos, personal communication, 2001). In 1998 a preliminary study carried out in Massachusetts suggested that plants grown under 60 % shade had the highest yields and the best quality (Carter A.K., personal communication, 2002).

Adequate nitrogen nutrition is imperative for the production of any crop due to its role in photosynthesis (Barker, 1979) and leaf expansion (Radin, 1983). The first increments of nitrogen added to the soil are always the most effective in terms of dry matter production and secondary product biosynthesis in herbs, with excess nitrogen fertilization often resulting in limited yields (Cox, 1992). The range of nitrogen requirements among herbs is broad. In the case of cilantro (*Coriandrum sativum* L.), an aromatic and botanical relative of ngo gai, nitrogen application in excess of 100 kg N/ha did not result in increased yields (Rangappa et al., 1997). The optimal nitrogen fertilization rate for lovage (*Levisticum officinale* Koch) was determined to be between 45 and 75 kg N/ha (Galambosi and Szebeni-Galambosi, 1992) and that of peppermint (*Mentha piperita* L.) was between 210 and 274 kg N/ha (Mitchell and Farris, 1996).

The nitrogen requirement of ngo gai had not yet been studied and due to economic and environmental concerns regarding nitrogen in agriculture, it is important to elucidate this requirement. Additionally, in many instances, the nature and extent of a plant response to shade is dependent on the nitrogen status of the plant and vice versa, so an understanding of these interactions is fundamental (Clabby and Osborne, 1997). Thus this research was conducted with the objective of creating a guide for growers in Massachusetts for the cultivation of ngo gai.

## **MATERIALS AND METHODS**

Ngo gai transplants were grown from seed (Richters Seed Co., Ontario, Canada) at a commercial farm (Harvest Farm, Whatley, Mass.). The seeds were started in Fafard mix (Fafard, Agawam, Mass.) and kept in a mist house at 23.9 C° with bottom heat at 23.9 C°. All of the seedlings had begun to produce flower stalks while still in the greenhouse and these were removed before transplanting. The experiment was implemented at the University of Massachusetts Research Farm in South Deerfield, Massachusetts, on an Occum fine sandy loam (coarse-loamy, mixed, mesic Fluventic Dystrochrept) with a pH of 6.7 and a soil organic matter content of 2.9 %. Available phosphorus and potassium in

the soil were high, according to a soil test, so no application of these elements was made. The soil was covered with a black polyethylene mulch to control weeds. The experimental design consisted of four replicate blocks. The shade treatments were assigned randomly within each block, and a randomized split plot design distributed the three nitrogen treatments within each shade treatment. Uniformly sized seedlings were transplanted to the field on 12 June 2001 (84 days after starting the seed) and irrigated with 200 mL water. There were 28 plants per treatment arranged in 4 rows of 7 with 15 cm spacing within and between rows. This arrangement of plants allowed for a border of plants to surround 10 central experimental (sample plants) plants for each plot. Rows were oriented in a north-south direction.

Shade treatments were applied following transplanting and were imposed as follows: 0 % (no cover), 20 % (spun bonded white polyester cloth, Reemay, Griffin Greenhouse Supply, Tewksbury, Mass.), 40 %, 60 %, and 80 % (woven black polypropylene shade cloth, A&M Leonard, Piqua, Ohio). Shade cloth was positioned at a height of 91 cm from the ground and centered across the row with a width of 91 cm so that it hung down 46 cm on either side of the row. Such a design was used to exclude any direct illumination and to obviate any microclimate alterations due to the presence of the shade cloth. Light meter readings were taken using a line quantum sensor (LI-188B, Li-Cor, Lincoln, Neb.) periodically at 1200 hr on cloudless days to verify the light reduction levels. Soil temperature probes (Fisher Scientific, Ottawa, Canada) were placed at a depth of 4 cm in each shade treatment, and the temperature was monitored weekly. Air temperatures for each shade treatment were also monitored weekly using a mercury thermometer.

The nitrogen was applied as a 300 mL aqueous solution of  $\text{NH}_4\text{NO}_3$  at 0 (control treatment), 45, and 90 kg N/ha, split over two applications. The first application was made the week after transplanting, and the second application was 4 weeks later. Every seven days any emerging flower stalks were removed and SPAD readings were taken. Flower stalks were weighed before and after drying. The recorded value of the SPAD readings for each plot was the mean of 10 readings (plants) in each plot, taken on the newest fully expanded leaves.

All of the plants were harvested at 60 days after transplanting. Leaf number, mass, and root mass were measured for each experimental plant in addition to the regular recording of flower production data (harvest occurred 11 days following the final weekly flower cutting). The number of 'decayed leaves' per plant (leaves that appeared to be either senescent or necrotic) was recorded at harvest. These leaves were excluded from the recorded leaf number counts. Leaf area was measured with a meter (LI-3100 Area Meter, Li-Cor, Lincoln, Neb.). Plants were ranked as either marketable (=1) or unmarketable (=0) based on the appearance and suppleness of the leaves. All plant parts were then oven dried at 80 °C until no further change in weight occurred, and dry mass was recorded.

Total leaf nitrogen was assessed using the modified Kjeldahl method (Bradstreet, 1965). Soil nitrate levels at time of harvest were determined colorimetrically by automated cadmium reduction (Technicon Autoanalyzer, Technicon, 1977). Results were analyzed using the SAS GLM, REG, MIXED, and CORR procedures (SAS Institute, Cary, NC). Growth analysis calculations used to determine specific leaf area, leaf mass ratio, and leaf area ratio were as outlined by Hunt (1978).

## RESULTS

The following discussion of results, unless otherwise indicated, refers to the fresh plant material. The soil and air temperature readings and rainfall recorded over the course of the experiment are given in Figure 1. A general decline in soil and air temperatures occurred with increasing shade. The readings from the light meter confirmed that the degree of light reduction (% shade) for each shade treatment was as advertised by the manufacturers of the shade cloth.

Flower production increased in the weeks following transplanting (Figure 2). Fewer and lighter flowers were produced under increasing shade. However, by week 5, the

greatest flower numbers were in plots with the 20 % shade treatment. At week 7, plants from the 40 % shade treatment had the greatest mass per flower. Highly significant interactions between shade and time were manifested at week 3 for flower numbers and at week 4 for flower mass. Flower numbers and mass decreased linearly over the shade treatments at these times and at each subsequent week. Nitrogen also had a significant effect on total flower mass per plant and average mass per flower but not on flower numbers with 45 kg N/ha ultimately resulting in the greatest values and 90 kg N/ha the lowest.

At harvest, flower numbers (Figure 3) and flower mass (Figure 4) exhibited inverse linear relationships to shade levels. The greatest number of flowers was at 0 % shade (8.9) and lowest was at 80 % shade (4.4). The greatest flower mass was 4.1 g/plant (0 % shade) and the lowest was 2.4 g/plant (80 % shade).

Total biomass per plant decreased linearly with increasing shade from 36.0 g/plant (0 % shade) to 12.5 g/plant (80 % shade) (Figure 5). In addition to the effect of shade, total biomass increased linearly with increasing nitrogen supply. The increase was from 23.4 g/plant (0 kg N/ha) to 27.4 g/plant (90 kg N/ha). No interaction was observed between shade and nitrogen on total biomass produced.

The number of leaves produced per plant decreased linearly with increasing shade from 72.4 (0 % shade) to 44.2 (80 % shade) (Figure 6). However, a significantly greater number of decayed and undesirable leaves were on the plants grown with less shade (Figure 6). At 0 % shade, the average was 17.8 decayed leaves per plant, whereas at 80 % shade the average was 4.8. Nitrogen treatments did not significantly affect leaf number or number of decayed leaves.

Total leaf mass per plant decreased linearly with increasing shade from 20 % (33.1 g/plant) to 80 % (17.2 g/plant). The nitrogen treatments had no significant effect on total leaf mass. Conversely, mean leaf mass was significantly affected by the nitrogen treatment but not by shade, increasing very slightly with a linear trend with increasing nitrogen rates. Mean leaf mass at 0 kg N/ha was 0.42 g/leaf and at 90 kg N/ha was 0.46 g/leaf. A significant interaction occurred between shade and nitrogen. At 20 and 40 % shade mean leaf mass increased progressively from 0 to 90 kg N/ha nitrogen with a quadratic trend ( $P=0.0002$  and  $P=0.0010$  respectively). However at 60 % shade, although with a quadratic trend in the increase ( $P=0.0455$ ), the difference between mean leaf mass at 45 kg N/ha (0.468g) and at 90 kg N/ha (0.465g) was negligible. Overall, the greatest mean leaf mass per plant resulted from 20 % shade and 90 kg N/ha treatments (0.52g).

The total leaf area per plant decreased with a significant quadratic trend as shade increased (Figure 7). Plants at 0 and 40 % shade had the same total leaf areas (645.7 cm<sup>2</sup>/plant). Plants at 20 % shade had the greatest total leaf area (724.5 cm<sup>2</sup>/plant) and those at 80 % shade the smallest (456.5 cm<sup>2</sup>/plant). Mean leaf area was affected by the shade (Figure 8) and nitrogen (Figure 9) treatments although no interaction occurred between these treatments. Leaves grown at 40 % shade had the greatest mean leaf area (11.3 cm<sup>2</sup>/leaf). The mean leaf area also increased significantly with increasing levels of nitrogen from 9.9 cm<sup>2</sup>/leaf (0 kg N/ha) to 10.7 cm<sup>2</sup>/leaf (90 kg N/ha).

The specific leaf area (total leaf area/total leaf dry mass) per plant increased linearly with increasing shade from 136.1 cm<sup>2</sup>/g (0 % shade) to 207.2 cm<sup>2</sup>/g (80 % shade) (Figure 10). The leaf mass ratio (total leaf dry mass/total plant dry mass) per plant increased with increasing shade with a quadratic trend. The range of values from 0 to 60 % shade was 0.45 to 0.50, with 80 % shade resulting in a value of 0.57. The leaf area ratio (total leaf area/total plant dry mass) per plant also increased significantly with increasing shade from 60.8 cm<sup>2</sup>/g (0 % shade) to 119.9 cm<sup>2</sup>/g (80 % shade). The ratio of leaf to total fresh mass increased significantly with increasing shade. The lowest ratio was 0.42 (0 % shade) and the highest was 0.55 (80 % shade) (Figure 11).

The increase in leaf quality ratings followed a linear trend, with quality improving as shade increased (Figure 12). Plants grown under 0 % shade had a quality rating of 0.03 whereas those grown under 80 % shade had a rating of 0.88. The dry matter content of the leaves significantly decreased with increasing shade from 15.98 % (0 % shade) to 12.85 % (80 % shade).

Results from the Kjeldahl tissue analysis of the leaves for total nitrogen displayed a linear trend in the mean total nitrogen content over the three nitrogen fertilization rates from 2.31 % (0 kg N/ha) to 2.45 % (90 kg N/ha). Mean SPAD readings per plot from the week of harvest had a significant linear decrease from 46.5 at 0 kg N/ha to 44.2 at 90 kg N/ha. There was no significant effect of shading on the SPAD readings. The nitrate levels of the soil at harvest increased with a linear trend with increasing fertilization rates from 17.5 mg/kg (0 kg N/ha) to 25.5 mg/kg (90 kg N/ha).

## DISCUSSION

To introduce ngo gai as a crop to Massachusetts, it is important to understand the dynamic nature of the environment that will affect its growth and development. In general, few interactions affecting growth and development were found between the two environmental factors under investigation, shade and nitrogen. This result was contrary to the findings of other authors who have reported significant interactions between light and nitrogen affecting plant growth and development (Clabby and Osborne, 1997; Eriksen and Whitney, 1981).

The effects of either shade or nitrogen on flowering over time did not become apparent immediately, indicating the time it took the plants to acclimatize to the imposed treatments. Flower production was somewhat suppressed at lower light levels, a finding that was consistent with the results of Santiago-Santos and Cedeno-Maldonado (1991) in a study on ngo gai and with other authors (Neumaier and Blessington, 1987; Nell et al., 1981; Virzo de Santo and Alfani, 1980) in studies on other species. Nevertheless even at the lowest light level, the plants continued to produce flower stalks that needed to be removed weekly. This would be time-consuming and costly for growers in Massachusetts. Flower primordia can develop very early in the lifecycle of a plant (Kim et al., 2000), and once floral development begins the process cannot be halted but merely delayed (Janick, 1986).

The obvious peak in flower production at week 4 may be related to a decrease in available soil nitrogen as the cuttings were taken before the second application of fertilizer to the soil. The drop to lower values recorded the following week supports this theory for the 45 and 90 kg N/ha treatments but does not explain the rise and drop in values for the 0 kg N/ha treatment. A more likely explanation would be that another environmental factor, or a combination of factors, may have contributed to the observed peak in flower production at week 4. The recorded air and soil temperatures from 11 July 2001 were the lowest for the entire duration of the experiment. The records available from the weather station at the Research Farm indicate that the daily maximum and minimum temperatures during the week between the third and fourth cuttings were relatively low with two troughs of low average daily temperatures occurring during that week. In addition, considerable rainfall during that period may have influenced flowering. Nothing in the literature relates the flowering of ngo gai to low temperatures; in fact, the opposite is suggested by growers who maintain that flowering is greatest during the summer months.

The total biomass of the plants clearly declined as the availability of light for photosynthesis and hence carbohydrate formation declined. This trend is consistent with research of other authors including Halva et al., (1992) in their studies on dill (*Antheum graveolens* L.). However, Virzo De Santo and Alfani (1980) found that dry matter production in mint (*Mentha X piperita* L.) was identical in full sun or 66 % shade. Such differing responses between species to light reduction highlights the varying adaptive capabilities of the species due in part to their respective ecological histories and other environmental factors (Eriksen and Whitney, 1981).

Santiago-Santos and Cedeno-Maldonado (1991) reported that the leaf mass of ngo gai produced under 63 or 73 % shade was greater than that produced under full sun. In this study, total leaf mass was greatest at 20 % shade. All other shade treatments resulted in values that were less than that for plants grown in full sun. The varying effects of light reduction on leaf mass in ngo gai may be due to the greater light intensity of full sunlight

at the low latitude of Puerto Rico. Alternatively, the differences may have been a reflection of inherent genetic differences in shade tolerance between the seed used in the two experiments.

The effect of increasing nitrogen supply on the increase in total biomass was an expected result since nitrogen is fundamental to the process of photosynthesis and biomass accumulation (Evans, 1983; Hilbert, 1989). The interaction of nitrogen fertilization rate with the shade levels resulted in a maximal average leaf mass at 20 % followed by 40 % shade at the highest nitrogen fertilization rate. At 60 % shade, light had become a limiting factor for leaf mass accumulation, and clearly the optimal fertilization level had decreased from 90 kg N/ha to 45 kg N/ha.

Vladimirova et al. (1997) examined the morphological plasticity of *Dracaena sanderana* hort Sander ex Mast. 'Ribbon' found a concomitant decline in number of leaves with increasing shade. A decline in leaf numbers with increased shading is a common observation (Halva et al., 1992; Santiago-Santos and Cedeno-Maldonado, 1991) that was also made in this study on ngo gai. The parallel observation that the numbers of decayed leaves declined as shade increased somewhat offset the effect of the reduction in leaf numbers. Since microbial infection was not evident in the decayed leaves, it is possible that the leaves had some phototoxicity at the higher light levels, which resulted in the apparent oxidative damage that rendered them unacceptable.

Ngo gai is sold by the bunch, each usually comprised of leaves from individual plants, rather than by weight. Since the market demands ngo gai with large leaves, manipulation of plant development to produce leaves of a large surface area is important. However, it is equally important to understand that leaf numbers per plant has a great influence on the economic viability of any such successful manipulations. Plants grown at 40 % shade had a markedly higher mean leaf area than in the other treatments. Urbas and Zobel (2000) noted in their studies that declining light levels generally resulted in a suppression of total biomass and leaf numbers but that the leaves generally tended to be thinner and have a greater leaf area. Pons (1977) found that the maximal leaf area produced by *Cirsium palustre* L. or *Geum urbanum* L. was at 32 % daylight but that the rate of leaf appearance declined significantly as the light level was reduced from full sun.

Mean leaf area of ngo gai was also influenced by nitrogen, increasing with the increase in nitrogen fertilization rates. Yoshida et al. (1969) attained increasing mean leaf areas in rice as they increased the nitrogen supply. Nitrogen plays an important role in leaf area expansion (Radin, 1983), and the role has been related to water stress imposed on nitrogen-deficient plants. Radin and Boyer (1982) postulated that the impact of nitrogen status on leaf area expansion, related to root hydraulic conductivity and leaf water relations, is mediated by its effect on membrane fluidity.

The increase in dry matter content of the roots and leaves with the increasing light levels is a phenomenon that has been observed by other authors as part of a typical shade response (Hughes, 1965). Inherent in the tolerant response of ngo gai to shade is the alteration, specifically the increase, in the specific leaf area. Such an increase in specific leaf area is a common feature of plants that are tolerant of shade (Givnish, 1987; Hughes, 1965; Virzo de Santo and Alfani, 1980) and serves to maximize the leaf surface area available for interception of the limited incident light. Partitioning of biomass is altered to provide the maximum possible surface area for photosynthesis (Loach, 1970; Pons, 1977). The increase in specific leaf area is attributed to the greater expansion of existing cells rather than increased cell division (Hughes, 1965). This observation is confirmed in this research by the decrease in dry matter content with increasing shade. Typically leaves grown in the shade have fewer layers of palisade parenchyma cells than leaves grown in the sun (Pons, 1977). In the current study, 40 % shade elicited a response of a similar magnitude as that for 60 % shade in terms of the dry matter content, which manifested itself in greater leaf area expansion. Therefore, 40 % shade conferred the double benefit of receiving enough light for greater biomass accumulation than 60 or 80 % shade coupled with relatively large morphological response to shade.

The increasing specific leaf area values of ngo gai that occurred with increased

shading contributed to the high quality of leaves observed in the shade-grown plants. Generally the plants grown at 0 and 20 % shade had thick and spiny leaves with the smallest leaf areas rendering them largely unmarketable. The other shade treatments resulted in leaves with higher specific leaf area values, lower dry matter contents, greater mean leaf area values, and hence higher quality.

Another index of quality and marketability of the leaves of ngo gai is the degree of greenness of the leaves since consumers prefer a dark green color. Tissue nitrogen contents increased with increasing nitrogen fertilization, and due to the fundamental role of nitrogen nutrition in the chlorophyll complex (Barker, 1979), one would expect green color to parallel the level of nitrogen nutrition. However, SPAD readings declined with increasing nitrogen fertilization. One possible explanation could be that since mean leaf area increased with increasing fertilization, the chlorophyll was more concentrated spatially in the smaller leaves. Light reduction had no significant influence on the green color of the leaves, an observation that is inconsistent with observations made by Santiago-Santos and Cedeno-Maldonado (1991) in their study on ngo gai. Other authors have also reported increased chlorophyll contents due to cultivation in shade (Virzo de Santo and Alfani, 1980). The general consensus on the increase in chlorophyll content of shade grown plants is that more resources are channeled into chlorophyll synthesis in the low light environment to maximize available light utilization (Virzo de Santo and Alfani, 1980).

## CONCLUSION

Ngo gai demonstrated significant adaptability to shading and some positive responses to nitrogen fertilization. Based on the results of this experiment it appears that cultivation under 40 % shade with a fertilization at a rate of at least 90 kg N/ha is optimal for field production of ngo gai in Massachusetts during the summer. Further studies should report the effect of the earlier imposition of shade to further suppress flowering and the effect of greater nitrogen fertilization rates than were used in this study.

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## Figures

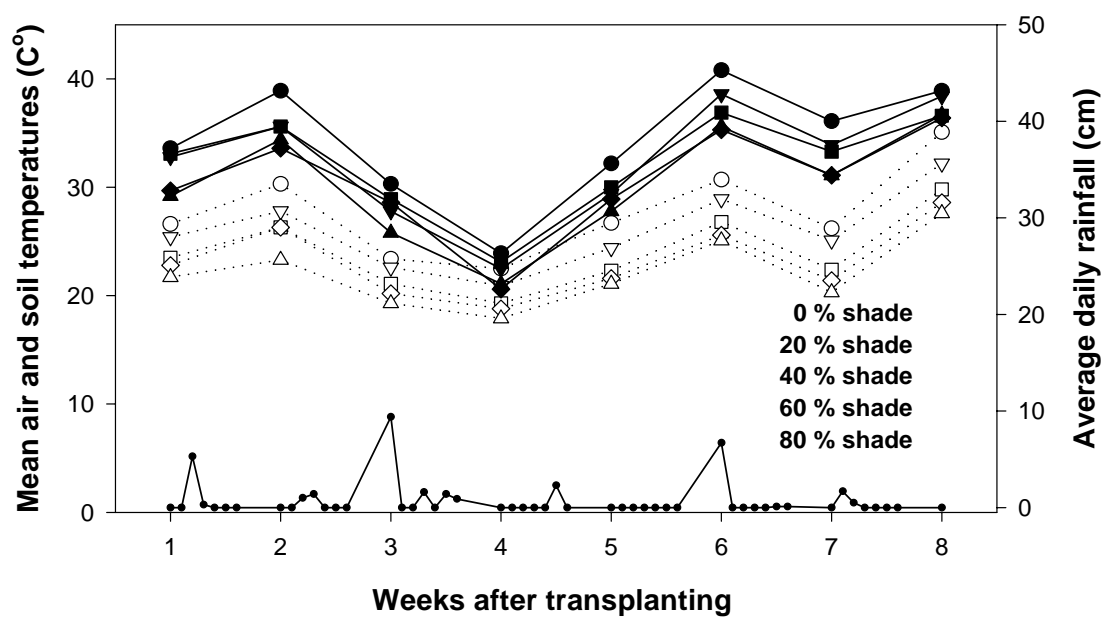


Fig. 1. Average daily rainfall (cm) recorded at the research farm and mean ( $n=2$ ) weekly mid-day air (solid symbol) and soil (open symbol) temperatures ( $C^{\circ}$ ) recorded at the light-reduction levels.

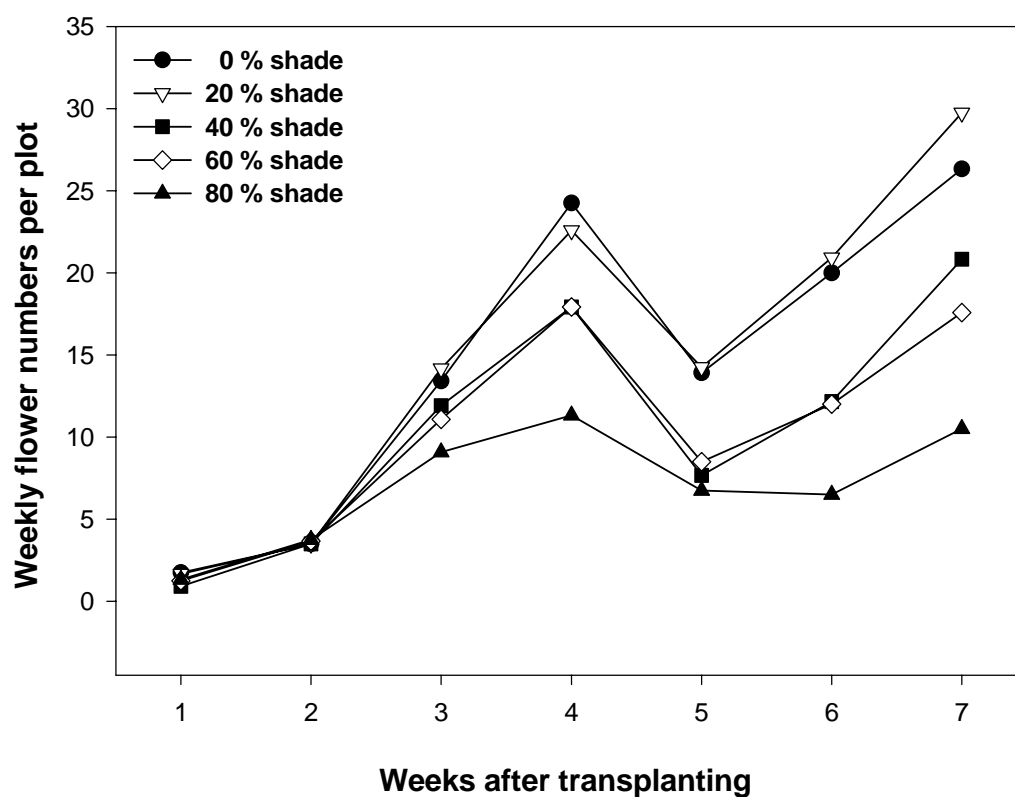


Fig. 2. Number of flowers at different light-reduction levels produced per plot (10 plants) as a function of time (means;  $n=12$ ).

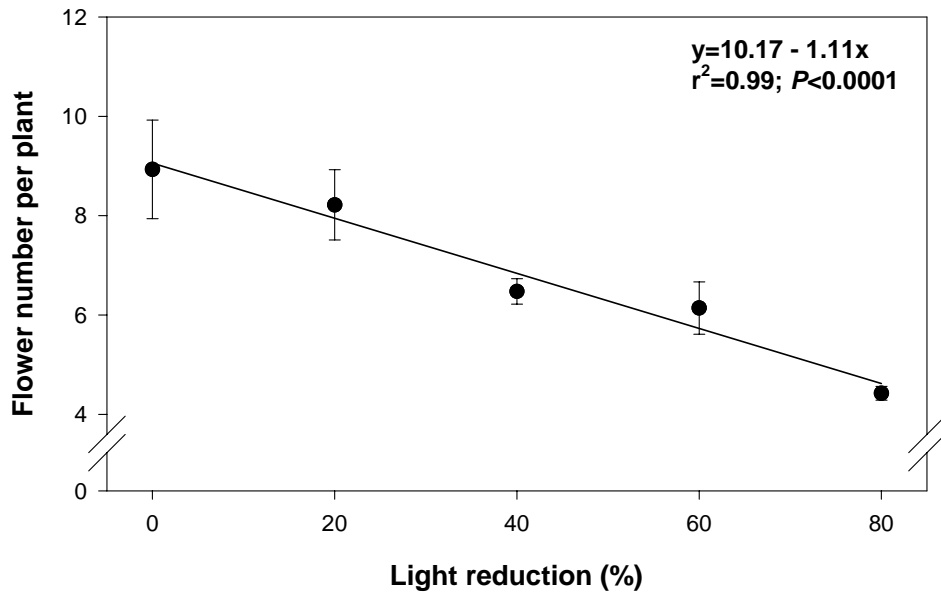


Fig. 3. Number of flowers per plant at harvest as a function of light-reduction levels (means; n=120; vertical bars represent the standard error of the mean).

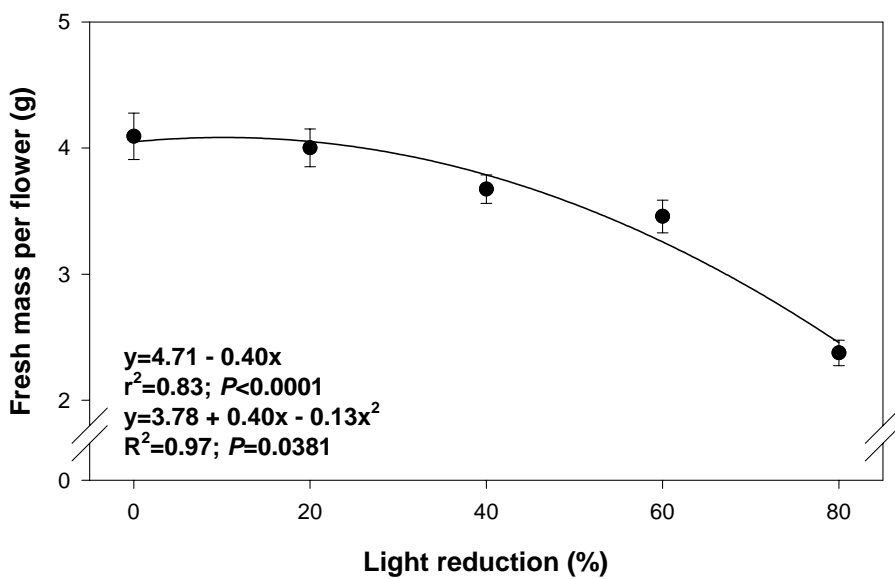


Fig. 4. Flower fresh mass per plant at harvest as a function of light-reduction levels (means; n=120; vertical bars represent the standard error of the mean).

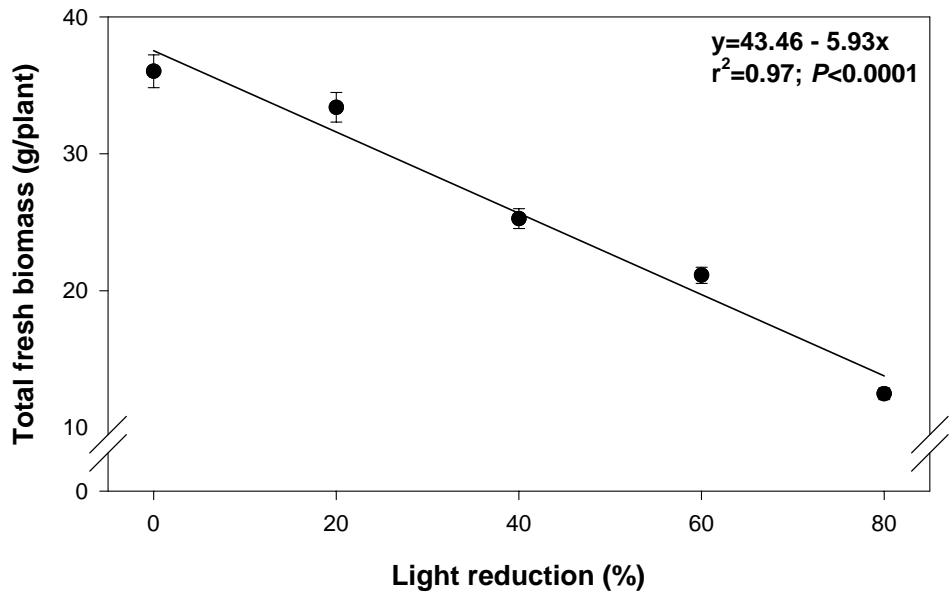


Fig. 5. Total plant fresh biomass at harvest as a function of light-reduction levels (means; n=120; vertical bars represent the standard error of the mean).

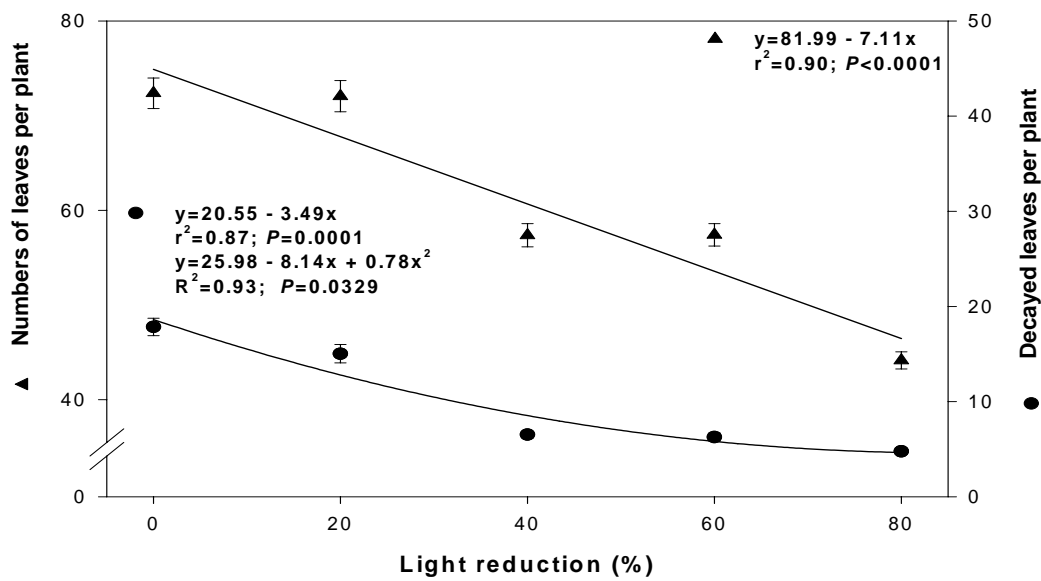


Fig. 6. Total leaf and decayed leaf numbers per plant at harvest as a function of light-reduction levels (means; n=120; vertical bars represent the standard error of the mean).

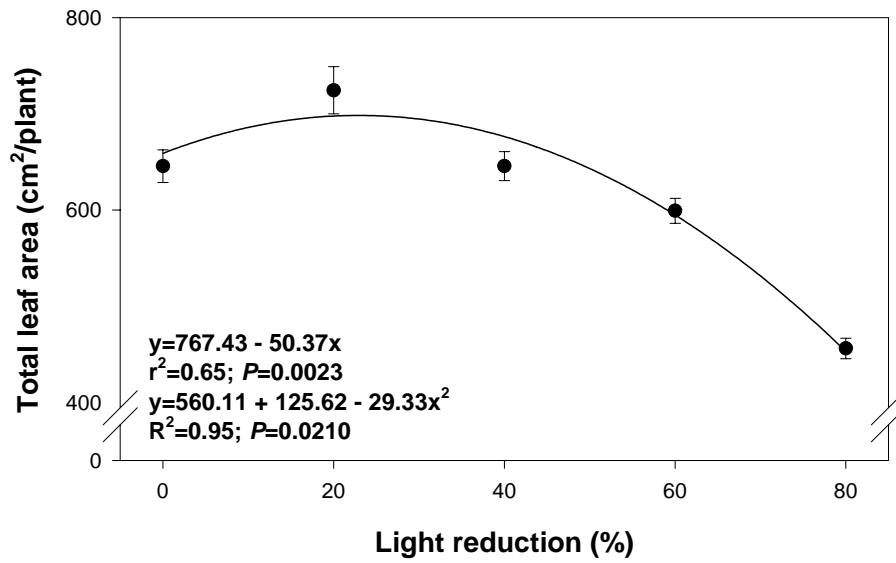


Fig. 7. Total leaf area per plant at harvest as a function of light-reduction levels (means; n=120; vertical bars represent the standard error of the mean).

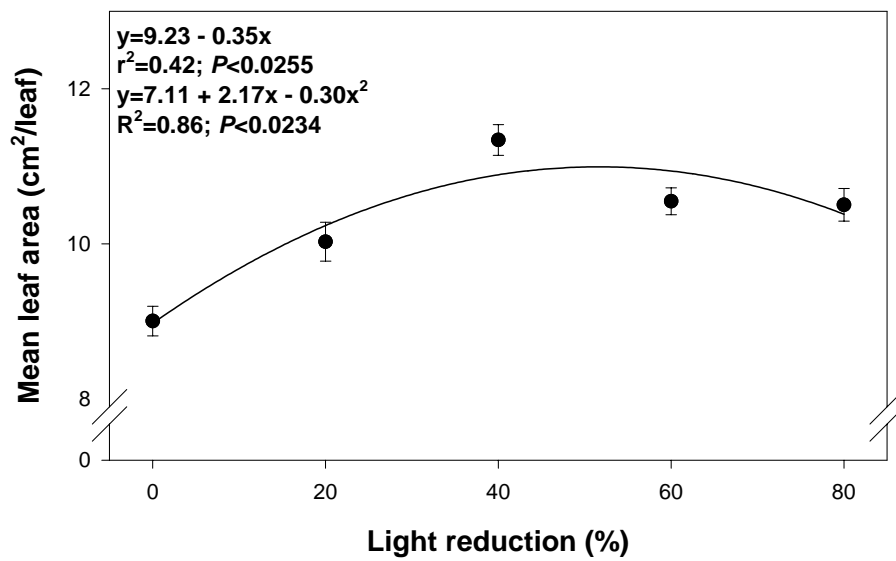


Fig. 8. Mean leaf area per plant at harvest as a function of light-reduction levels (means; n=120; vertical bars represent the standard error of the mean).

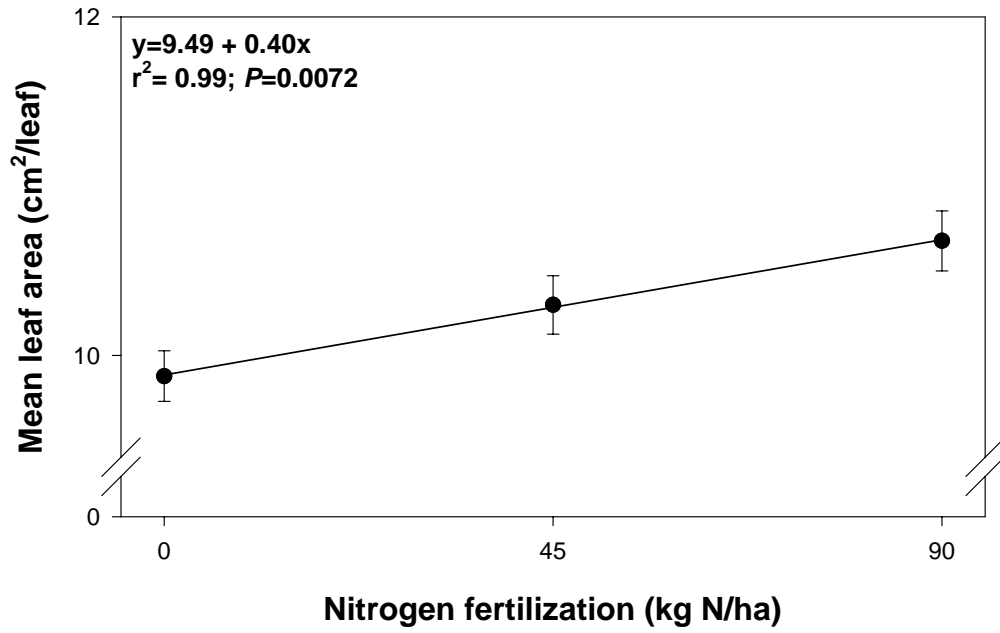


Fig. 9. Mean leaf area per plant at harvest as a function of nitrogen fertilization rates (means; n=200; vertical bars represent the standard error of the mean).

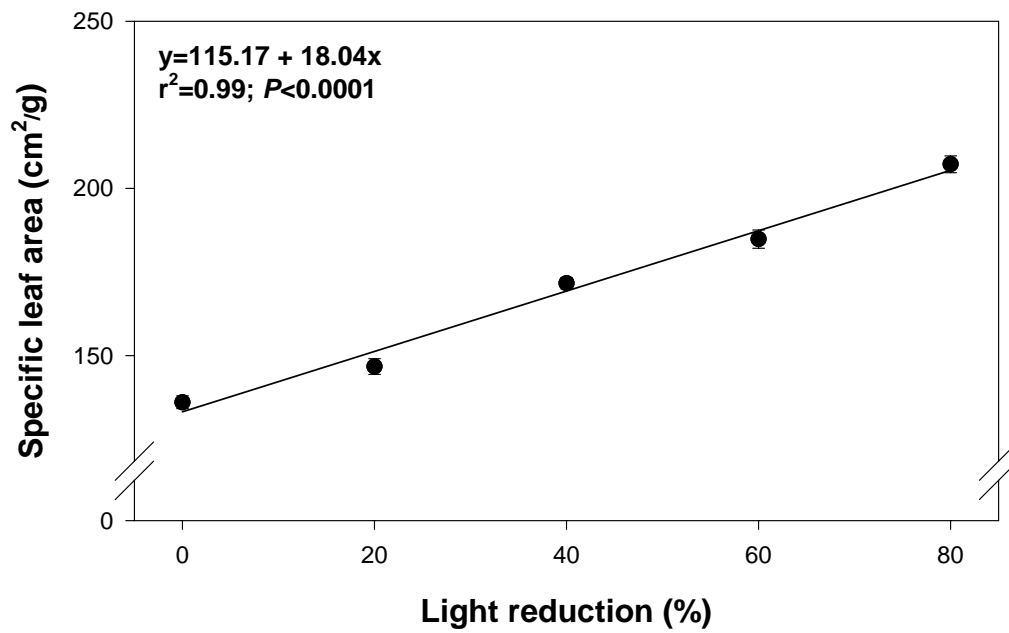


Fig. 10. Specific leaf area per plant at harvest as a function of light-reduction levels (means; n=120; vertical bars represent the standard error of the mean).

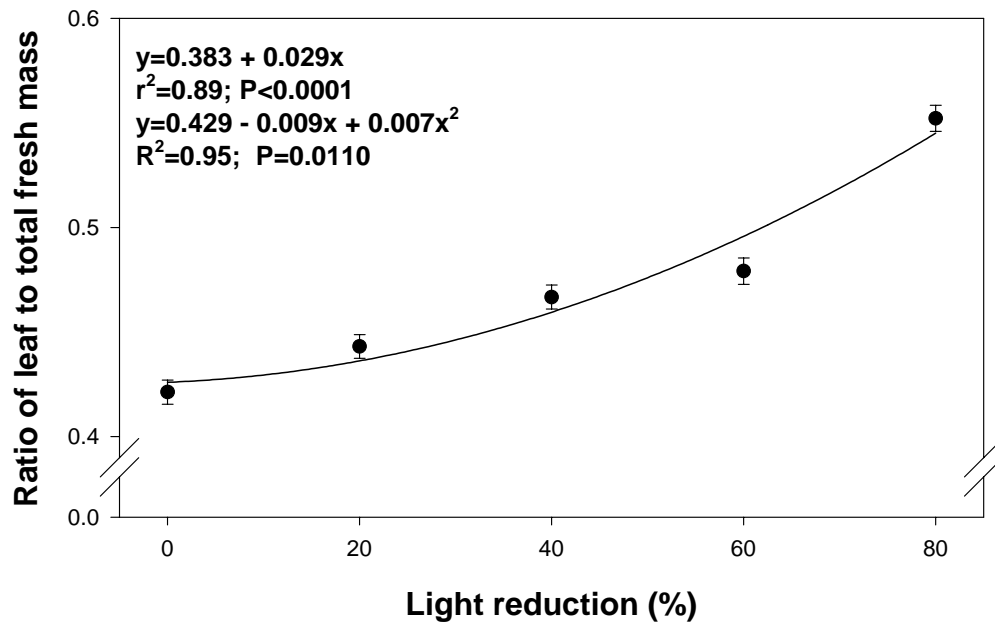


Fig. 11. Ratio of leaf to total fresh mass per plant at harvest as a function of light-reduction levels (means; n=120; vertical bars represent the standard error of the mean).

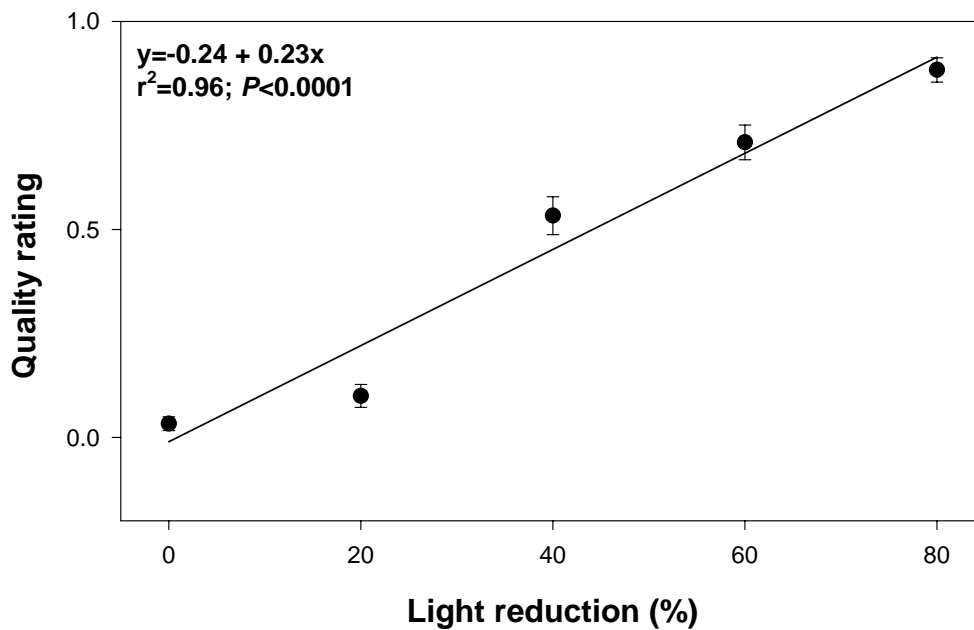


Fig. 12. Leaf quality of plants at harvest as a function of light-reduction levels (means; n=120; vertical bars represent the standard error of the mean).