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Production, seeds and carbohydrate contents of cape gooseberry (*Physalis peruviana* L.) fruits grown at two contrasting Colombian altitudes

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Summary

In the Boyacá region (5°N 73°W) of Colombia, cape gooseberry ecotypes 'Kenya', 'South Africa' and 'Colombia' were grown at 2,300 and 2,690 m altitude above sea level during 10 months. With increasing altitude a reduction in fruit production was observed, principally through the smaller fruit number, whereas fruit weight units were not affected. The two African ecotypes developed heavier fruits but with a smaller fruit number per plant compared to those of the Colombian origin. The greatest harvest peak at 2,300 m was obtained five months after planting (128 fruits/plant) and decreased continuously during the following pickings. At 2,690 m highest harvest peak was obtained 10 months after planting (78 fruits/plant). Elevation also influenced fruit development, which lasted 75 days at 2,690 m and 66 days at 2,300 m. Percentage of dry matter and sucrose accumulation in fruits increased with decreasing altitude. Fruit glucose and fructose contents remained unaffected by the altitudinal factor. At the high location, fruits produced a smaller number and weight of seeds.

Introduction

Cape gooseberry (*Physalis peruviana* L.) originates from the Andean highlands of South America. It belongs to the family Solanaceae, in which the genus *Physalis* includes about 100 species, which form their fruits in an inflated calyx (LEGGE, 1974). In many parts of the Andes, cape gooseberries grow wild up to 3,000 m above sea level (FAO, 1982). The plant productivity in poor soils, easiness of cultivation, and low requirement for water and fertilizer has made it an attractive potential crop (MCCAIN, 1993). In Colombia, it is not only an important source of vitamins (A and C) for the highland farmers, but also has become the second important export fruit (FISCHER et al., 2005). The tropics are known as the zone of thermal uniformity without marked seasons in all altitudes. LAUER (1986) states clearly that temperature has the main effect on altitude classification of tropical mountains. Thus, RUNDEL et al. (1994) denominate the climate in tropical alpine environments as having summer every day and winter every night. BARCELO et al. (2001) characterized high elevations as regions with high light intensity, low temperature, great diurnal temperature fluctuations, frequent situations of drought, and low CO₂ and O₂ partial pressures. Among these, high ultraviolet radiation has been demonstrated to have profound effects on field crops (KAKANI et al., 2003).

Growth, production, and quality of fruits are strongly influenced by tropical altitude (FISCHER, 2000). Climatic factors, especially temperature and light intensity, have a strong influence on the nutritional quality of fruits and vegetables, but the effect of site elevation on fruit quality has been studied only in few cases (SCHAFER and ANDERSEN, 1994). Lulo (*Solanum quitoense*) develops fruits in Andean regions of 15-16°C mean temperature in 140-160 days, but with increased temperatures of 17-20°C the duration of fruit development may be only 120-130 days (ERASO, 1991). Peach

varieties, grown at higher elevations (2,500 m) in Mexico, delayed their harvest season from 20 to 40 days (PEREZ, 2001). FISCHER et al. (2000) found that two altitude conditions in Colombia, 2,300 and 2,690 m, had no effect on organic acid (citric, malic, tartaric, and ascorbic acid) accumulation in cape gooseberry fruits, but, in contrast, β-carotene and total provitamin A carotenoids were significantly higher at the lower altitude. Temperature during fruit growth and maturation influenced quality by either hastening or delaying horticultural maturity (ARPAIA, 1994).

Final fruit size is influenced by various factors and is determined by the genetically fixed cell number and also genetically contributed capacity of cell elongation dependent on the environmental conditions (FRIEDRICH and FISCHER, 2000). Developing seeds play an important role in fruit development (CRANE, 1969). Seeds are centers of metabolic activity (DENNIS, 1984), and once have initiated seeds development these seem to exert a predominant effect on fruit growth in many species.

Although fruit growth and ingredient accumulation are affected by tropical altitude markedly, there is no information about the influence of the tropical altitudinal microsite conditions on growth, seeds, and non-structural carbohydrate contents of cape gooseberry fruits growing on the slopes of the Colombian East Cordilleras. Results of the present ecophysiological study help to make this crop better known and ready for genetic and cultural-technical improvements. The Colombian highland farmers will be able to select appropriate locations for cropping *Physalis* in order to enhance fruit production and improve its nutritional quality.

Material and methods

The ecotypes 'Colombia', 'Kenya' and 'South Africa' were propagated by seeds and transplanted after 10 weeks into experimental fields in Villa de Leyva at 2,300 m and Tunja at 2,690 m, both locations in the Boyacá department (5°N 73°W) of Colombia. The climate conditions at 2,300 m were: 17°C mean air temperature, 19.5°C mean soil temperature, 66.6% relative humidity (RH), 837 mm annual precipitation, 5.3 daily sunshine hours, and 148 mW UV-B radiation. At 2,690 m, the climate conditions were: 12.5°C mean air temperature, 16.8°C mean soil temperature, 79% RH, 302 mm annual precipitation, 5.3 daily sunshine hours, and 160 mW UV-B radiation. Because of the close distance to the equator, the monthly mean air temperature oscillated only between 16.6 and 17.9°C at 2,300 m and 11.0 and 15.1°C at 2,690 m during the 44 weeks of the growing period. During a period of 24 hours, the leaf temperatures in the surrounding air, inside the calyx and the soil (10 cm depth) were measured.

The cape gooseberries were planted at a distance of 1 x 1 m and supported with a V-frame system. The soil at both sites was sandy loam with a corrected pH value of 5.7 and an organic matter content of 4.5%. Fertilization, irrigation, plant protection, and pruning

practices were applied according to local procedures. A polyfactorial block design was used with three replicates on two locations. Data was analyzed using the SAS program to determine least significant differences (LSD).

Fruits were harvested when skin color turned from light-orange to orange, indicating the physiological maturity (FISCHER et al., 1997). Seeds were taken from mature fruits, counted and weighed to evaluate the site and ecotype effect.

Fruits were picked between 7.00 to 8.00 a.m., and these used for sugar analysis immediately frozen. Sucrose, glucose, and fructose contents were determined by high-performance liquid chromatography (HPLC) using Waters Associates 6000A pump, U6K Universal injector, R-401 differential refractometer, and Waters UV/VIS photo diode array detector. For separation, Bondapak C18 column (10 μ m, 30 x 0.39 cm) was used. Isocratic separation of sugars was achieved at 20°C using acetonitrile:water ratio 83:17. Injecting 30 ml, the flow rate was adjusted to 1.2 mL·min⁻¹. Sample preparation was made following the method of GANZEDO and LUH (1986). Each sample consisted of six replicates representing 20-25 g fruit FW. Total carbohydrates were defined as the sum of sucrose, glucose, and fructose.

Results

Fruit development

Fruit development appeared to be affected slightly by the altitude (Fig. 1) and followed a sigmoid curve with a marked increase in diameter during the first 20 days reaching nearly 65% of their final size at this early stage. Up to 30 days of development, there was no observed effect of the altitudes on fruit diameter, after which fruits at the low elevation grew faster and presented significantly greater diameters than those at the high site, especially between 50 and 60 days of development. At harvest, after 70 days, fruits at the 2,690 m site had reached nearly the same size as those at 2,300 m, because of their over-proportional growth during the last stage (Fig. 1).

After 70 days, fruit diameter at the low site was still higher than at the 2,690 m location as a main effect (Fig. 1). Fruits of South African plants were 2.5 cm, significantly the largest, and those from Colombia with 1.9 cm were the smallest among the three origins (Tab. 1).

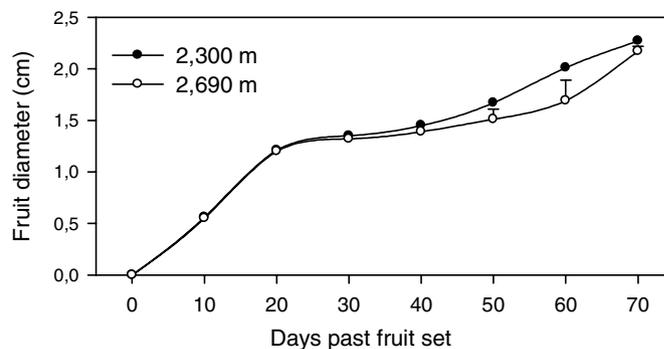


Fig. 1: Influence of the altitude (2,300 and 2,690 m) on the development of fruit diameter of three cape gooseberry ecotypes during the experiment in Colombia; vertical bars indicate significant differences (LSD) at $P < 0.05$.

The altitude exerted significant effects on the duration of fruit development (observed past fruit set), however this parameter appeared to be unaffected by the plant origin. At the 2,690 m site, fruit development lasted about 75 days, but only 66 days at the low site (Tab. 1).

The African types needed significantly more time to complete fruit development than the Colombian ecotype. As in all other studied yield components, the Colombian type did not show any altitude dependence, not even in the period of fruit development (Tab. 1).

Tab. 1: Effect of the altitude (2,300 and 2,690 m) on the fruit dry matter accumulation, fruit development period, fruit number and fruit yield of three cape gooseberry ecotypes in Colombia; different letters indicate significant differences (LSD) at $P < 0.05$.

Parameter	Altitude (m)	Ecotype			Mean altitude
		Kenya	S. Africa	Colombia	
Fruit development (days)	2,300	63 d	66 d	70 c	66 B
	2,690	75 ab	77 a	72 bc	75 A
Fruit diameter (cm)	2,300	2.31 b	2.56 a	1.86 c	2.24 A
	2,690	2.21 b	2.45 a	1.84 c	2.17 B
Fruit DM accumulation (%)	2,300	17.5 bc	21.7 a	19.6 ab	19.6 A
	2,690	16.3 c	16.5 c	18.5 bc	17.1 B
Unit fruit weight (g)	2,300	6.5 a	6.8 a	4.1 c	5.8 A
	2,690	5.9 b	6.7 a	4.3 c	5.6 A
Fruit number/plant	2,300	226 cd	292 b	383 a	300 A
	2,690	156 e	190 de	348 a	231 B
Fruit yield (kg FW/plant)	2,300	1.468 b	1.970 a	1.564 b	1.667 A
	2,690	916 c	1.230 b	1.494 b	1.213 B

Fruit dry matter accumulation

In general, more dry mass was accumulated in fruits at the low altitude, than in those at the 2,690 m site (Tab. 1). Kenyan plants not only had the least fruits, but also the lowest dry matter accumulation comparing the three ecotypes. On an average, the Kenyan and the Colombian ecotypes appeared to have exactly the same fruit dry mass accumulation.

The South African ecotype accumulated a considerably higher dry mass in fruits at the 2,300 m location (Tab. 1) causing the altitude mean difference. The other two ecotypes only showed tendencies towards this behavior.

Fruit production

The effect of altitude on **fruit weight unit** was less than on yield, but ecotype differences were more noticeable with this parameter. Fruits produced by the Colombian type had a markedly lower (35%) unit weight than the others (Tab. 1). The South African origin developed significantly highest fruit weight unit.

Comparing interaction means, a pronounced altitude effect was only produced by the Kenyan ecotype (Tab. 1), which had significantly higher fruit weight unit at the lower location (2,300 m). Conversely, the Colombia ecotype tended to have heavier fruits at the high altitude.

The accumulated **fruit number**, harvested until the end of the experiment in May, differed significantly with the altitude, similar to the yield, but also with the plant origin. As a main effect, with lowering the altitude from 2,690 to 2,300 m, significantly more fruits were picked (Tab. 1). At its native site, the Colombian ecotype produced a noticeably higher fruit number than the two African types, 48% more fruits than the Kenyan and 34% more than the South African. Nevertheless, from latter origin more fruits were picked than from Kenyan plants.

With increasing altitude, harvested **fruit fresh weight** decreased markedly as a main effect (Tab. 1). Comparing the three ecotypes, main effect means showed uniformly higher fruit fresh weight of the South African and Colombian plants than of the Kenyan type.

As an interaction, only harvested fruit weight of the African origins was significantly higher at the 2,300 m site compared to that of the 2,690 m location (Tab. 1). The fruit production of the Colombian ecotype remained unaffected by the factor altitude. At the 2,690 m site, South African cape gooseberries produced a clearly heavier fruit yield than the Kenyans, however, at this site, Colombian plants had highest fruit production of the three ecotypes used.

Fruit harvest course

With reference to the fruit harvest course, realized between November and August, this parameter was significantly affected by the altitude. At the 2,300 m site, the first fruit harvest in December was the highest one (128 fruits/plant), then showed a progressively decreased production in two further harvest peaks, which followed at two-month intervals (Fig. 2). After the last peak in April (50 fruits/plant), production declined and finally increased once more, but slightly, from June to August (12 → 30). Conversely, at 2,690 m, fruit numbers picked in December and January were very low (11 and 12 fruits/plant, respectively). In May, highest fruit numbers (78 fruits/plant) were collected at this high site, but afterwards production decreased dramatically in July (6 fruits) and then increased up to 21 fruits in August.

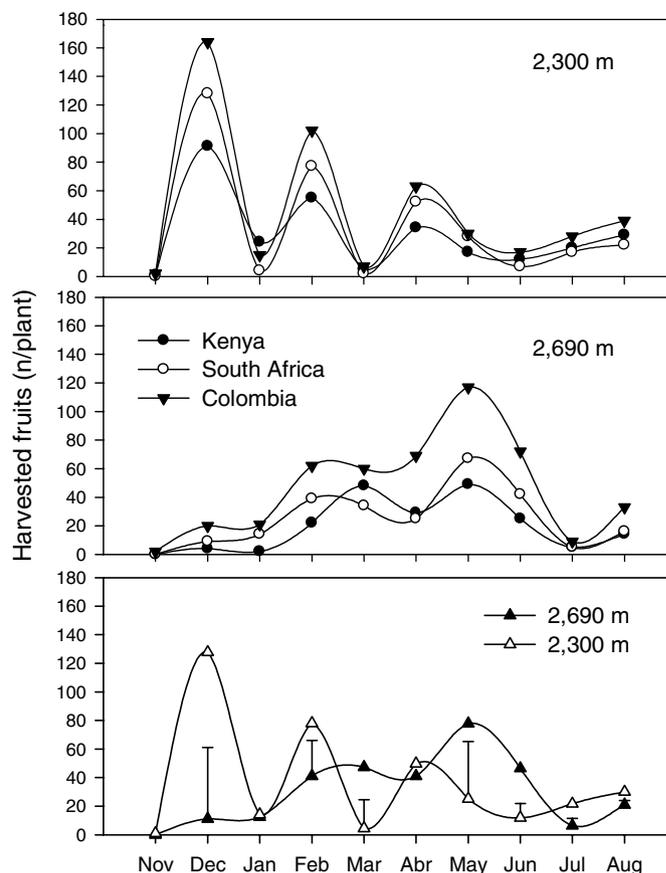


Fig. 2: Effect of the altitude (2,300 and 2,690 m) on the course of harvested fruits during the experiment in Colombia (means of three cape gooseberry ecotypes); vertical bars indicate significant differences (LSD) at $P < 0.05$.

Seed content

Seed number and seed weight differed greatly with altitude and the ecotypes used. In general, number of seeds per fruit and g fruit FW, as well as seed weight per fruit and per unit, increased significantly with lowering the altitude from 2,690 to 2,300 m (Tab. 2). In regard of the total seed weight per fruit, differences between the locations were most distinct. Fruits at the low site had a 28% higher seed weight than those at the high altitude. However, the parameter seed weight unit was only slightly affected by the site factor.

South African fruits not only developed remarkably higher total seed weight, but also much heavier unit seeds than the two other ecotypes. Unit seeds from South African fruits were more than twice as heavy as these of Colombian fruits. In respect of the seed number per fruit, the Kenyan type had significantly higher values than the others. However, Colombian fruits contained markedly most seeds per gram fruit FW.

Although the low altitude increased all recorded seed components, such as seed number and weight per fruit, as well as unit seed weight and number per g fruit, only the Kenyan ecotype reacted with a significant increase in fruit weight. The only small differences related to the unit seed weight and seed number per gram fruit between the two locations make apparent that altitude did not exert a sufficient influence on the seeds to induce different fruit weights (Tab. 1, 2).

Tab. 2: Effect of the altitude (2,300 and 2,690 m) on the fruit seed content of three cape gooseberry ecotypes in Colombia; different letters within the same column indicate significant differences (LSD) at $P < 0.05$.

Altitude (m)	Ecotype (origin)	Fruit g FW	Seed			
			n fruit ⁻¹	mg fruit ⁻¹	mg unit ⁻¹	n g ⁻¹ fruit
2,300	Kenya	6.0 b	348 a	320 c	0.92 c	58 b
	South Africa	7.7 a	277 c	459 a	1.65 a	36 d
	Colombia	4.9 c	312 b	234 de	0.73 e	66 a
	Mean ecotypes	6.2 ns	312 A	388 A	1.10 A	54 A
2,690	Kenya	5.7 b	292 bc	269 d	0.92 c	51 c
	South Africa	7.1 a	249 cd	380 b	1.52 b	35 d
	Colombia	4.6 c	245 d	197 e	0.80 d	53 c
	Mean ecotypes	5.8 ns	262 B	282 B	1.08 B	47 B

Carbohydrate composition

Glucose content was modified by the ecotypes and was affected by the altitude only in interaction with the plant origin. The Colombian ecotype accumulated significantly more glucose in the fruits than the African types did; both the latter had similar glucose values. As an interaction, with increasing altitude Kenyan fruits contained markedly more glucose, although South African and Colombian ecotypes were not affected by the elevation (Fig. 3).

Similar to glucose the **fructose** content was also not clearly dependent on the altitude, but noticeably on the ecotype and strong interaction effects were observed. As with the glucose, Colombian fruits also contained most fructose compared to the African ecotypes. As an interaction, Kenyan fruits accumulated significantly more fructose at the 2,690 m altitude than at the low site, whereas for Colombian fruits it was exactly the opposite (Fig. 3).

Sucrose accumulation in fruits was significantly related to the altitude and the ecotype. With decreasing altitude, sucrose content

increased, as a main effect. Fruits from the Kenyan ecotype concentrated remarkably more sucrose than those from South Africa. Colombian fruits had intermediate sucrose values. Further examination of the interaction effect shows that with increasing altitude sucrose content of the two African ecotypes was significantly reduced; the native type Colombia only showed a tendency towards this reaction (Fig. 3). Fruit sucrose content increased with decreasing altitude, whereas analyzed monosaccharides, glucose, and fructose remained unaffected. The parallel increase of fruit dry matter accumulation (Tab. 1) indicates that sucrose is the principal component of fruit dry matter.

Total carbohydrate content remained unaffected by the altitude; however, it was significantly related to the ecotype. In general, the Colombian and Kenyan ecotypes accumulated more carbohydrates in fruits than the South African. At both locations, the Kenyan ecotype concentrated remarkably more total carbohydrates in fruits than the South African origin (Fig. 3).

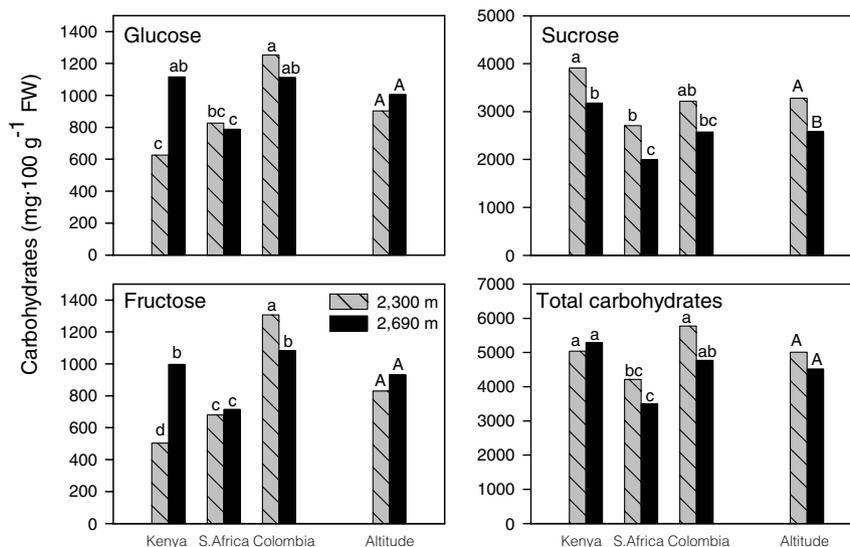


Fig. 3: Effect of the altitude (2,300 and 2,690 m) on the glucose, fructose, sucrose, and total carbohydrate content of fruits of three cape gooseberry ecotypes in Colombia; different letters indicate significant differences (LSD) at $P < 0.05$.

Discussion

Fruit development and production

In regard of fruit diameter growth, the high yielding African ecotypes utilized the site advantage more efficiently and began 30 days before harvest to increase fruit size faster than at the high altitude. However, fruit diameter and fruit weight unit was only slightly affected by the altitude. Probably, the mean air temperature of 12.5°C at the high elevation site was not sufficient enough to affect these parameters more, which is in agreement with AGUSTI (2004), who indicated that, generally, temperatures below 10°C decrease fruit diameter.

Fruit development period of the two African ecotypes was prolonged by nearly 3 days for each 100 m of altitude increase. Similarly, but more drastically each 100 m of altitude increased growth cycles in banana by one month (SAMSON, 1986). Peach varieties grown at higher elevations (2,500 m) in Mexico showed harvest season delays from 20 to 40 days (PEREZ, 2001). Also 'Valencia' oranges, grown in the Trujillo state of Venezuela, showed accelerated fruit growth rates at lower altitudes as compared to the higher located zones (ZAMBRANO and QUINTERO, 2001).

Dry matter accumulation in fruits was increased at 2,300 m, which may indicate higher sink strength or a more efficient translocation of photosynthates as compared with the high altitude field. According to BROWN (1984), the yield potential of a crop is viewed as a product of the photosynthate produced and the fraction of photosynthate diverted to the fruit. Factors known to reduce plant growth, such as low temperatures, water stress, and mineral nutrient deficiencies, also reduce translocation (FRIEDRICH and FISCHER, 2000). The low temperatures at the high location, especially night air temperatures and soil temperatures may explain the declined dry matter allocation to fruits and, on the other hand, the longer fruit development period.

Regarding fruit set and, therefore, fruit number produced, a critical night temperature has to be taking into account. In tomatoes, the optimal range for fruit set lies between 15 and 20°C (VARGA and BRUINSMA, 1986), so that night temperatures recorded at the high altitude of between 5.7 and 13.0°C can have limited fruit set of the cape gooseberries. Although the critical night temperature for fruit set in cape gooseberries is still unknown, we observed (data yet not published) a normal fruit set in these species at air temperatures of 12°C, but growth rate and thereby fruit setting were obviously slowed as compared to the 19°C regime.

It appears that the higher air temperature regime at the low altitude (2,300 m) with a mean temperature of 17.4°C and a mean maximum of 20.5°C hastened vegetative growth and reproductive maturity (KINET et al., 1985) as compared to the high elevation with 12.5 and 15.1°C, respectively. FISCHER et al. (2005) established a mean growth temperature between 13 and 18°C as optimum for cape gooseberries. With reference to EVANS (1975) it appears evident that the duration of photosynthetic optimal temperatures during the day is more important than the daily mean temperature. Thus, cape gooseberry plants at the low altitude received supposed optimal temperatures $\geq 20^\circ\text{C}$ for 9 hours per day as compared to only 5 hours at the high elevation.

In the altitude experiment, an effect of the root zone temperature cannot be excluded. Although soil temperature at the 2,690 m site had a mean value of 16.8°C, the recorded minimum of 13.0°C was four degrees lower than that at 2,300 m. Similar to own findings under glasshouse conditions, in where 15°C root zone temperature reduced fruit number markedly as compared to 22°C (FISCHER and LÜDDERS, 1992), the low soil temperatures $\leq 15^\circ\text{C}$ during 15 hours

per day at 2,690 m could have contributed to a shorter shoot growth (lower node number) and, thereby, a reduced fruit set.

A close relationship between yield and vegetative plant parts in cape gooseberry was also found by ASNA et al. (1988), who recorded a high correlation between fruit yield and leaf width as well as plant height. These findings correspond well with our results, demonstrating that the higher yielding plants at the 2,300 m site had larger leaves recorded during all readings and plants were higher, especially during first 24 weeks of experiment (FISCHER and LÜDDERS, 2002). In tomatoes, fruit weight and volume were also positively correlated with the leaf area per fruit (STENVERS and STADEN, 1976), however total yield depended mainly on the number of fruits. These findings agree completely with the present results.

With regard to the two monthly production peaks at the low altitude, this seems to indicate that marked new fruit setting only took place when fruits were fully developed or already harvested. This corresponds with the findings of BROWN (1984), who indicated that when a plant develops a heavy fruit load, the fruits seem to have priority for the photosynthates over vegetative plant parts. Thus, when fruit terminates its intensive sink activity growth, shoot elongation and fruit set increases (FRIEDRICH and FISCHER, 2000). In the present study, after harvesting the fruits (removal of the sinks) again an elongation growth of shoots could have taken place and new fruits were induced in the developing nodes. MARCELIS (1993) found an increased leaf production in cucumber when number of fruits decreased.

The higher number of fruit bearing nodes at the lower elevation affected yield significantly, taking into account that, for the December harvest, the shoot length, which was built in October when fruits were set, was more than 3.5 times higher at 2,300 m than at the 2,690 m location (FISCHER and LÜDDERS, 2002).

The recorded yields of 1.7 kg/plant until May and 2.1 kg/plant (correspond to 21 t·ha⁻¹) during one year at the 2,300 m site are in the reported international range, although increased harvests are possible through the application of trellis systems (FISCHER et al., 2005).

Plant yield has been considered a result of photosynthetic (source) capacities on the one hand and capacity to utilize photosynthate (sink activity) on the other (BROWN, 1984). In plants with indeterminate growth habit such as cape gooseberry, in which reproductive and vegetative growth occurs simultaneously, the two components may compete for photosynthetic products. Although higher NAR were recorded at the 2,690 m site (FISCHER and LÜDDERS, 2002), fruit yields expressed as fruit fresh weight per plant were higher at the 2,300 m location, in particular for the African ecotypes. Yield potential at the lower site were, however, less higher because of higher unit fruit weights, but rather through an increased fruit number. The higher fruit number for plants at 2,300 m was particularly due to the elongated shoot development with increased numbers of fruit-bearing nodes, at least during first 32 weeks of the experiment.

Seed content

Many studies have shown a link between seed number, berry development, and sugar and acid content (COOMBE, 1989; BOSELLI et al., 1995). There exist a marked correlation between the number of seeds and the final fruit size (Crane, 1969). The development of seed and fruit are strongly coordinated by hormonal signals, which are originated in the seeds (SCHOPFER and BRENNICKE, 2006).

In two grapevine cultivars, the final size of the berry was related to its seed number: one seeded berries were smaller than 2-3-4 seeded berries (BOSELLI et al., 1995). These data can be confirmed in our study comparing the Colombian and Kenyan ecotype, but not with the South African that had lower seed content, but a much higher fruit weight than the Colombian origin. Probably, in the South African ecotype, hormone production of the heavier seed attracted a higher amount of carbohydrates than in the other types.

FRIEDRICH and FISCHER (2000) stated that a strong basipetal flow of auxins results in that fruit develops a high capacity of attraction for fotoassimilates and mineral elements and so can grow more than fruits containing only few seeds. Thus, HO (1992) observed that seeded tomato fruits accumulate more dry matter and compete better for assimilate than fruit with fewer or no seeds.

In tomato, VARGA and BRUINSMA (1986) concluded that the growth of tomato fruit is not directly caused by cell elongation in the pericarp due to seed-produced indol acetic acid, but rather by indirectly profiting from the sink activity exerted by the developing seeds.

In agreement with results of VARGA and BRUINSMA (1986), who observed that tomato fruits with a lower seed number took more time in developing, we found the same tendency in the cape gooseberries growing at the 2,690 m altitude (Tab. 1, 2), but there, certainly, the lower temperature exerted its effect too on amplifying fruit development period.

Studying the same three cape gooseberry ecotypes grown in the 2,464 m high Nuevo Colón municipality in the Colombian Boyacá department PEÑA and AYALA (2006) found that 'Colombia' ecotype presented the highest seed index (number of seeds/100 g fruit weight) and had the most important relationship between the fruit fresh weight and the weight of seeds per fruit ($r^2 = 0.87$).

Carbohydrate composition

Like the majority of edible fruits, cape gooseberry contains three major sugars, i.e. sucrose, glucose, and fructose (SUGIYAMA et al., 1991).

The increased sucrose amounts at the warmer site (2,300 m) point out that there is a positive relation between the temperature and translocation rates of this sugar (BROWN, 1994). GUARDIOLA and GARCIA-LUIS (1993) stated that a lower organ temperature can increase the viscosity of the phloem solution and, thereby, reduce transport rates. In the present experiment, sucrose content was especially high in Kenyan fruits as the only ecotype, which produced significantly greater fruits and highest seed number at the 2,300 m site as compared to 2,690 m. Thus, it seems that temperature affected the translocation of assimilates into the fruit largely through its effect on the organ with the greater demand for assimilates (WARDLAW, 1980).

KOZŁOWSKI (1992) points out that the capacity of reproductive structures to import carbohydrates varies with the growth characteristics of the fruit, besides plant age and vigor as well as time of the experiment. With the higher seed content at the lower altitude there could be an increased sink capacity of these fruits, which in turn allows a higher inflow of sucrose (FRIEDRICH and FISCHER, 2000).

Ripening berries are a strong sink for solutes from photosynthesis and reserve organs (COOMBE, 1989). This relationship has been attributed to hormones such as auxins, gibberellins and cytokinins

formed in the seeds and spread into the pulp, thus promoting cell division and extension and modifying pulp composition (SCIENZA et al., 1978).

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