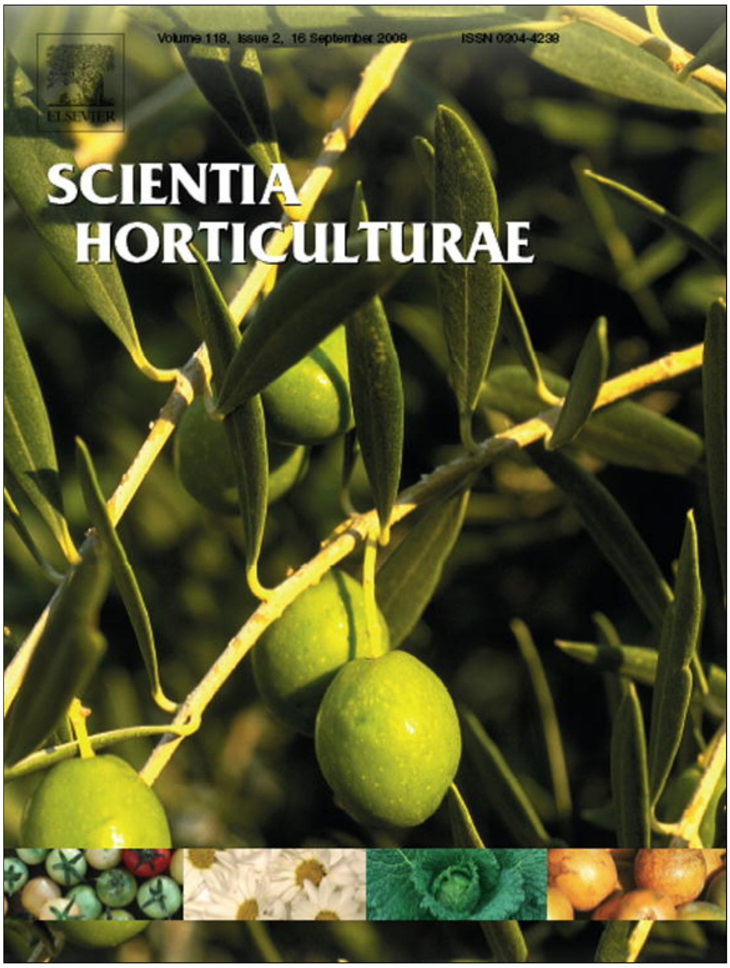
Volume 119, Issue 2, 16 September 2008
ISSN 0304-4238
ELSEVIER
SCIENTIA
HORTICULTURAE

Scientia Horticulturae 118 (2008) 100–105

Contents lists available at ScienceDirect

Scientia Horticulturae

journal homepage: www.elsevier.com/locate/scihorti

Photosynthesis of field-grown Arracacha (*Arracacia xanthorriza* Bancroft) cultivars in relation to root-yield

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ARTICLE INFO

Article history:
Received 28 June 2007
Received in revised form 29 April 2008
Accepted 27 May 2008

Keywords:
Arracacha
Apio
Breeding
Photosynthesis
Root-yield
Specific leaf area

ABSTRACT

There has been limited research on measuring potential differences in leaf gas exchange of Arracacha (Peruvian parsnip, *Arracacia xanthorriza* Bancroft) cultivars, as affected by different environments, as well as its relation to storage root-yield. The present paper reports field measurements of leaf CO_2 assimilation rates (*A*) for five contrasting cultivars grown at two different high-altitude locations. Using a design of plots chosen at random with three repetitions, commercial root production was determined in the two locations at different altitude (1580 and 1930 m). Daily leaf gas exchange was repeatedly monitored with a portable open-mode infrared gas analyzer at different times in both locations during the growth cycle. Root-yield, leaf area and dry weight were measured. Significant differences in leaf photosynthetic rate and in specific leaf area (SLA) were observed among cultivars. Cultivars with high SLA, had high CO_2 assimilation. Mean (A_n) and total (A_{tot}) of CO_2 assimilation and SLA were significantly correlated with storage root-yield across cultivars and locations. The three cultivars with the greatest commercial root production also had the highest maximum values for *A* and the highest specific leaf area, indicating that these two parameters can be used to select for highly productive cultivars of *A. xanthorriza*.

1. Introduction

Arracacha (*Arracacia xanthorrhiza* Bancroft) is a root vegetable whose nutritional value and various commercial possibilities have not yet been thoroughly developed and exploited in most Central and South American countries (Montaldo, 1991). In Venezuela, according to the records of the Ministry of Agriculture (MAC, 1996), the average national annual production of Arracacha in the period 1992 to 1996 was approximately 21 500 t. Seventy percent of the total production came from highlands of the Venezuelan Andes, a trend that remained constant for the last 25 years.

A typical feature of most farmer's cultural practices with this crop is the use of a mixture of cultivars, especially those with white and yellow roots. In various areas of cultivation there is always a mixture of autochthonous and introduced cultivars. These farmer's traditional practices were not based on precise knowledge of how different cultivars react to variations in the texture and nutritional qualities of soils. Information on root-yield for each cultivar is limited (Pineda, 1988; Noguera, 2001) and usually consists of the national total reported production. In addition, relevant physiological information is very limited in Arracacha (Hermann, 1997; Libreros, 2001). This deficiency of information hinders the evaluation, selection and improvement of yields. There have been programs for improvement and selection in Brazil taking into account yield, disease resistance, culinary features and durability after harvesting (Giordano et al., 1995).

Some physiological characteristic, for example harvest index (economic root-yield/total biomass) and leaf area duration, have been utilized as rapid and nondestructive tools in tropical root crops breeding programs such as in cassava (El-Sharkawy, 2004, 2006a,b). Net photosynthetic rate (*A*) has been a common criteria to identify possible lines of genotypes adapted to specific environment and with higher yield (El-Sharkawy, 2006b). Such evaluations have been done with crops such as cassava (El-Sharkawy et al., 1990; El-Sharkawy, 2004, 2006a,b), asparagus (Faville et al., 1999; Ball and Kelly, 1999), maize (Crosbie and Pearce, 1982), soybean (Dornhoff and Shibles, 1970; Ashley and Boerma, 1989) and peas (Mahon and Hobbs, 1981). Some modern cultivars used today have higher *A* associated with that of their predecessor also is correlated with higher yield (Blum, 1990; Morrison et al., 1999; Gutiérrez-Rodriguez et al., 2000). However, poor correlation between *A* and yield have been reported in barley (Berdahl et al., 1972), and oilseed rape (Chongo and McVetty,

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Abbreviations: *A*, net photosynthetic rate; A_n, mean CO_2 assimilation; A_{tot}, total daily assimilation of CO_2; A_{max}, maximum CO_2 assimilation; *E*, transpiration; g_s, leaf conductance; dap, days after planting.

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doi:10.1016/j.scienta.2008.05.027

2001). In some cases even negative correlation existed between maximum leaf photosynthesis and productivity (Evans, 1993). Nonetheless, Lawlor (1995) pointed out that there are some contradictions in the results for different crops in this respect because, limiting environmental and plant factors for yield and photosynthesis interact strongly. Therefore, it is important to evaluate optimal environmental conditions and better understand the mechanisms underlying biomass production under a range of conditions. There has been no evaluation of variations in the rate of photosynthesis that may correlate with root production in *Arracacia xanthorriza*. However, root-yield was significantly correlated with A in large accessions of cassava under field conditions in several locations and altitudes (El-Sharkawy et al., 1990; El-Sharkawy, 2004, 2006a,b).

It will be useful to know if high yields of Arracacha are related to high rates of assimilation or if they are independent of root production owing to variations in the distribution patterns of assimilates among different plant organs. The purpose of this research was to evaluate the relationship between root production in *A. xanthorriza* and the rate of CO_2 assimilation in five contrasting cultivars currently used in the Venezuelan Andes and to see if the assimilation rate can be used as an indirect factor to select highly productive cultivars. As far as we know this is the first comparative study of varieties of Arracacha involving gas exchange characteristics and their relationship to root production under field conditions.

2. Materials and methods

Two experiments were conducted in two different agroecological systems. The first experiment was carried out near Capuri (8°10′N, 71°35′W), 1580 m a.s.l. Average annual precipitation is 1140 mm and the annual mean temperature 19 °C (Noguera, 2001). The second experiment was at the Universidad de Los Andes, Agricultural Research Station, Santa Rosa (8°38′N, 71°10′W) 1930 m a.s.l. Mean annual precipitation is 2039 mm and the annual mean temperature 17.1 °C (Jaimez et al., 2001). Both locations are in the state of Mérida, Venezuela. Five cultivars of *A. xanthorriza* were used: *Bandera* (Ban), *Cebollo* (Ce), *Chamero* (Cha), *Cacho Buey* (Cb), *Bayuelo* (Ba). All but Bandera (white roots) have yellow roots. Further information and descriptions of these cultivars can be found in Faillace et al. (1972) and Noguera (2001).

The propagules were planted on June 20, 2001 and September 12, 2004 in Capuri and Santa Rosa, respectively. Propagules were planted at 0.50 m intervals between plants and with 0.40 m between rows in both locations according to Añez et al. (2001). A complete randomized block design with three replicates was used. Each plot had 42 plants. Fertilizer was applied 40 days after planting (dap) using 600 kg per hectare of commercially produced 12–12–17–2, following recommendations of Añez et al. (2002). Plants were watered every 5 days during dry periods in both locations.

2.1. Leaf gas exchange and growth

Net CO_2 assimilation (A), transpiration (E) and leaf conductance (g_s) measurements were made at 90 and 151 in Capuri and at 75, 97,124, 182, 253 and 305 dap in Santa Rosa on fully expanded leaves (five plants of each cultivar, randomly selected from the plots) every two hours using a portable open gas exchange system (LCA-4, ADC, England). Integration curves of daily CO_2 assimilation (from 8:00 to 15:30 h) were carried out to obtain total daily assimilation of CO_2 (A_{tot}) (Rada et al., 1996). Micrometeorological measurements were carried out simultaneously. Air and leaf temperature were measured with Chromel–Alumel thermocouples (36 gauges). Relative humidity was measured with a digital humidity meter (Extech instrument). These variables were used to determine leaf to air vapor pressure difference (VPD). Additionally photon flux density (PFD) was measured with a sensor on the leaf chamber of LCA-4. Measurements were made at ambient CO_2 concentrations between 340 and 365 μmol mol^{-1} in both locations.

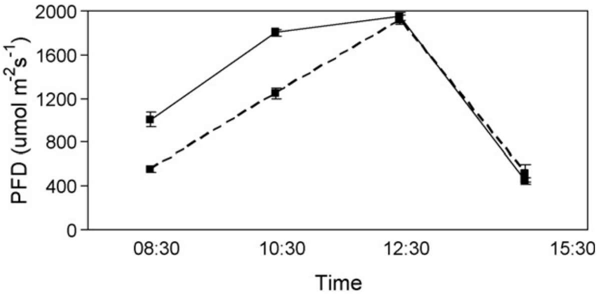

Fig. 1. Averages of photon flux density (PFD) during sunny days at Capuri (– – –) and Santa Rosa sites (—). Bars correspond to one standard error from mean.

Plant growth measurements were taken at the Santa Rosa site. Harvests dates corresponded to the same days gas exchange measurements were done. For each harvest, three adjacent plants were selected following the IBSNAT methodology (IBSNAT, 1990). Plants were separated into leaves, stems and root. The leaf area was measured using a leaf area meter (LICOR 1200). Dry weight per plant of all components (leaves, stems, and roots) were obtained after oven-drying at 70 °C to constant weight. In these experiments, evaluation of commercial root-yield (roots weighing more than 70 g) and total yield were conducted. The last harvest was carried out at 449 and 306 dap in Capuri and Santa Rosa, respectively.

Regressions were done between assimilation rates (mean CO_2 assimilation, (A_n), maximum CO_2 assimilation (A_{max}) and $A_{tot,}$) and root-yield in order to examine variations between cultivars. Production data was analyzed with ANOVA and the differences between cultivars were obtained using Tukey test ($p < 0.05$).

3. Results

PFD close to 1950 μmol m^{-2} s^{-1} were obtained at noon for both locations. After 15:00 PFD declined to 450 μmol m^{-2} s^{-1} due to cloud formation which happens frequently in high Andean locations (Fig. 1). Air temperature varied from 20 to 26 °C at Capuri and 22 to 27 °C at Santa Rosa. The highest relative humidity was obtained in Santa Rosa (Table 1). Leaf temperature varied between 20.0 and 27.4 °C for plants at Santa Rosa and between 19.1

Table 1
Mean maximum and minimum air temperature and relative humidity during measurement period (8:30–15:30 h) for the two study sites. Standard error from the mean in parenthesis

Location	Minimum temperature (°C)	Maximum temperature (°C)	Minimum relative humidity (%)	Maximum relative humidity (%)
Capuri	20.3 (0.4)	26.6 (0.3)	55.8 (1.3)	82.3 (0.8)
Santa Rosa	22.3 (0.5)	27.2 (0.5)	52.2 (0.4)	92.5 (2.0)

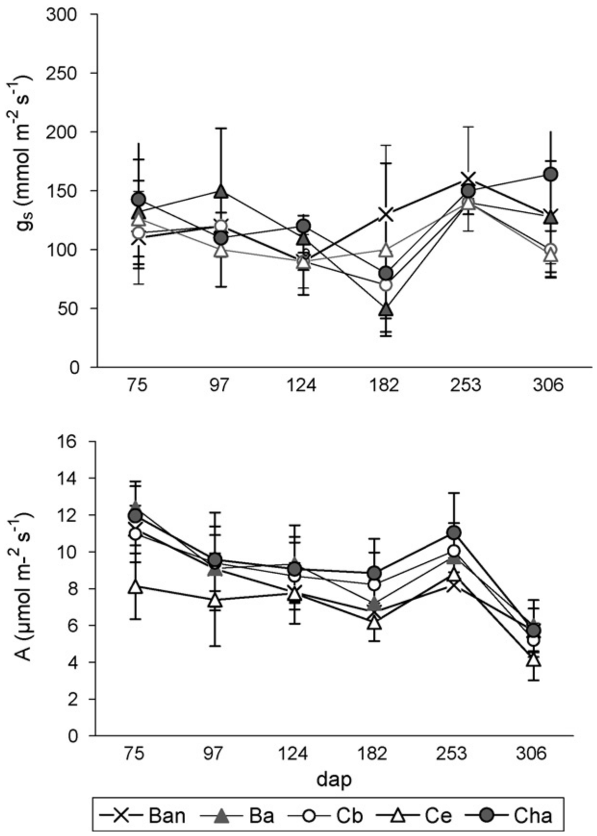

Fig. 2. Average of leaf conductance and CO_2 assimilation during life cycle of *Arracacia xanthorrhiza* cultivars: Bandera (×), Bayuelo (▲), Cacho (○), Chamero (●), and Cebollo (△) at Santa Rosa (1930 m). Bars correspond to one standard error from mean.

and 28.3 °C for plants at Capuri. VPD values varied between 1.2 and 3.4 kPa while gas exchange measurements were carried out at Capuri and Santa Rosa.

Daily averages of g_s of cultivars were between 95 and 150 mmol m^{-2} s^{-1} during most days of the cultivation cycle at Santa Rosa. A significant decrease was observed in g_s for cultivar Ba at 182 dap increasing the following days (Fig. 2). In Capuri, g_s averages for all cultivars were higher (140–270 mmol m^{-2} s^{-1}, data not shown). Arracacha cultivars maintained relatively constant daily average assimilation of CO_2 (A_n) with variations that did not surpass 4 μmol CO_2 m^{-2} s^{-1} until the 253 dap. All cultivars showed a 30% decrease in A_n daily averages at the moment of the final crop measurements having no relation to g_s reductions. Cultivar Ceb showed lower A_n averages throughout the cultivation cycle with maximum rates below 8.5 μmol CO_2 m^{-2} s^{-1}. Cultivar Ban showed a tendency to decreases A_n averages after 124 dap (Fig. 2). Highest CO_2 assimilation averages were close to 12.5 μmol CO_2 m^{-2} s^{-1}. Although there was about 50% difference in A_n among cultivars, the lack of significance in this case points to the need of measuring larger samples of leaves to partly overcome individual variations.

There were no differences in the growth of roots among cultivars until the 124 dap. Starting at 182 dap the cultivars Cb and Cha presented accumulations of dry matter in their roots that were three times of that accumulated in the other three cultivars. These larger dry root weights of Cb and Cha, continued until the end of the cultivation cycle (Fig. 3). These two cultivars had the largest root-yields (224 and 215 g dry weight per plant).

There was a tendency toward greater root-yield, both commercial and total, as the average maximum CO_2 assimilation rates increased. Linear and significantly positive relations were also obtained among the A_n and A_{tot} averages with averages of dry root-yield per area at the final harvests (Fig. 4a and b). There were significant linear relations between averages of maximum CO_2 assimilation rates and fresh root-yield at both locations (Fig. 5). There were significant differences in the average A_{tot} among cultivars. The values of A_{tot} ranged from 162 to 224 mmol CO_2 m^{-2} d^{-1}. However, there was no observed significant differences in A_n among cultivars. Therefore, the apparent

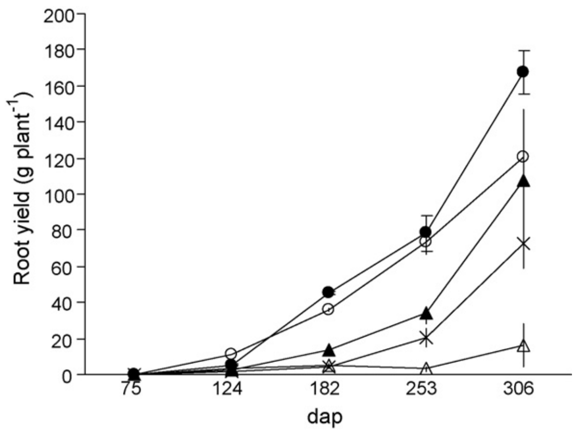

Fig. 3. Dynamics of dry root-yield during successive stages of development of five cultivars of *Arracacia xanthorrhiza* at Santa Rosa (1930 m). Symbols are the same as Fig. 2. Bars correspond to one standard error from mean.

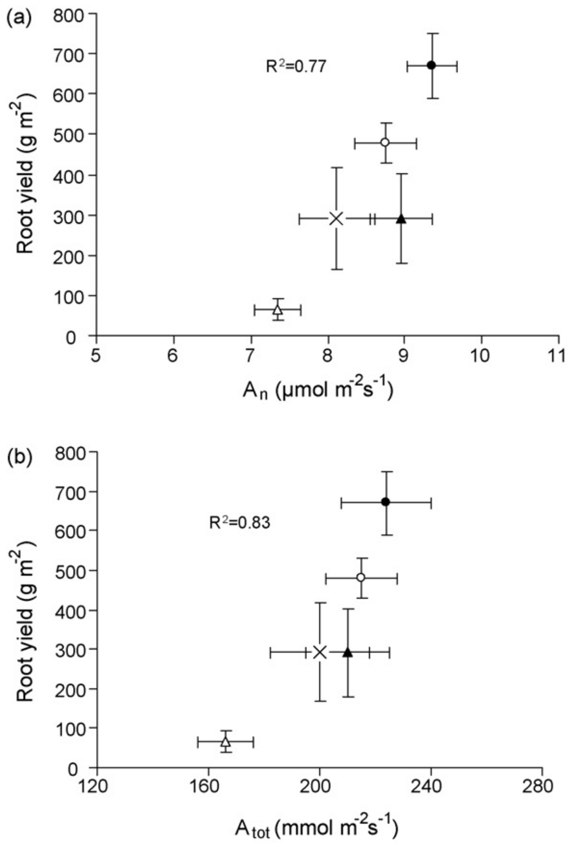

Fig. 4. Relationship between (a) average assimilation rates of CO_2 (A_n, μmol m^{-2} s^{-1}), (b) total assimilation rates ($A_{tot,}$ mmol m^{-2} d^{-1}) and dry root-yield, for five cultivars of *Arracacia xanthorrhiza* at Santa Rosa location (1930 m). Vertical and horizontal bars correspond to one standard error from mean. Symbols are the same as for Fig. 2.

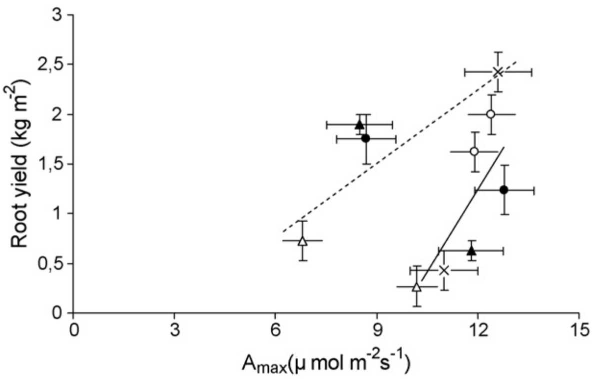

Fig. 5. Relation between fresh root-yield and maximun CO_2 assimilation rate (A_{max}) for cultivar of *Arracacia xanthorrhiza* in Capuri 1580m (– – –) and Santa Rosa, 1930 m (—). Vertical and horizontal bars correspond to one standard error from mean. Symbols are the same as Fig. 2.

cumulative differences in A_n across the day have led to larger differences in integrated daily assimilation rates.

Highest SLA in most cultivars were reached at 124 dap. decreasing gradually afterwards (Fig. 6). Similar to assimilation of CO_2, SLA showed a positive linear relationship with the root-yield. This relationship started 253 dap (Fig. 7).

The commercial fresh root-yield ranged from 0.43 to 2.73 and 0.35 to 1.6 kg m^{-2} in Capuri and Santa Rosa, respectively. Greatest total root production in Capuri was obtained from the cultivar Ban (2.43 kg m^{-2}), while Ceb had the smallest yield (0.43 kg m^{-2}), a difference of 68%. This indicates that Ban adapted better to this region. There is a preference for yellow root cultivars, such as Cb and Cha in the Capuri area, these being the most economically important cultivars in the area (Noguera, 2001). These showed no significant differences in commercial or total root production with respect to Ban. Commercial root production ranged from 82 to 89% of total root. Cultivar Ban was affected and its root production was very similar to cultivar Ceb in Santa Rosa area. However, Cha and Cb maintened the largest root-yield and Ceb the smallest (Table 2). The other cultivars maintained similar trend in terms of yield rank at both locations. Lower fresh root-yields were obtained in Santa Rosa compared to Capuri for all cultivars (Table 1).

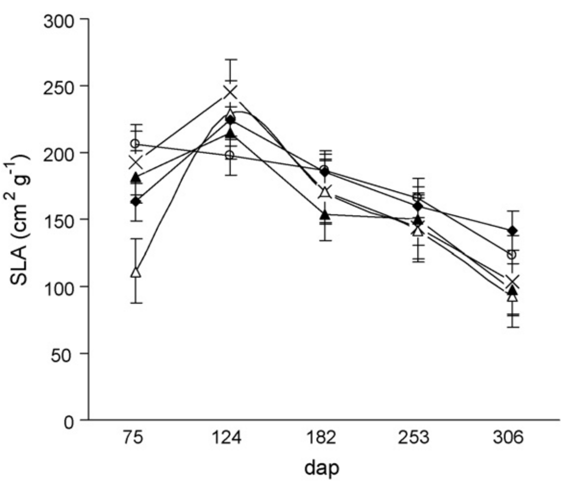

Fig. 6. Dynamics of specific leaf area for five cultivars of *Arracacia xanthorrhiza* during successive stages of development at Santa Rosa (1930 m). Bars correspond to one standard error from mean. Symbols are the same as for Fig. 2.

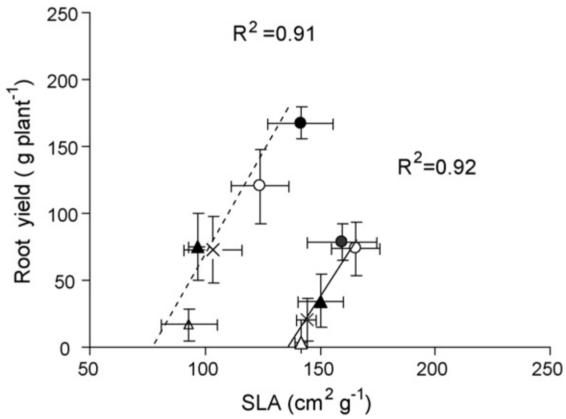

Fig. 7. Relation between dry root-yield and specific leaf area for five cultivars of *Arracacia xanthorrhiza* at 253 dap (—) and 306 dap (– – –) in Santa Rosa (1930 m). Symbols are the same as Fig. 2.

Table 2
Average commercial fresh root-yield (kg m^{-2}) of the Arracacha cultivars in Capuri (1580 m) and Santa Rosa (1930 m), Mérida state, Venezuela

Cultivar	Capuri	Santa Rosa
Bandera	2.23 a	0.43 b
Bayuelo	1.84 ab	0.63 b
Cebollo	0.93 c	0.27 c
Cacho Buey	2.00 a	1.62 a
Chamero	1.75 ab	1.24 a

Different letters within the same column indicate significant differences between means, Tukey test ($p < 0.05$).

4. Discussion

Results indicate that Arracacha cultivars are affected by variations in edafoclimatic conditions. Ban cultivar showed higher root-yield at Capuri and about a 50% reduction in yield at Santa Rosa. In contrast, other cultivars showed similar rank of root-yield. Ca and Cha showed a higher root-yield while Ce had the lowest root-yield at both locations. Reductions in yield of all cultivars at Santa Rosa might be attributed to the higher precipitation registered in this location. Ban was the most sensitive cultivar to excesses in soil water. In both trials fungal diseases were controlled and there were no observed disease symptoms in the storage roots at final harvests. Thus, reduction in yield at Santa Rosa was not probably due to root damage and root rot. Since A_{max} tended to be higher across cultivars at Santa Rosa, as compared with rates at Capuri, excess rainfall might have produced less assimilate partitioning to storage roots. Wardlaw (1990) has reported that low temperatures affect and produce changes in the distribution of assimilates among the different organs. It is possible that lower growth rates were associated to low temperatures.

Arracacha cultivars showed that allocation of assimilates to root occurred between 120–182 dap. This agree with results reported by Pineda (1988) for Arracacha in Venezuela. The relationship between SLA and root-yield might be due to variations in the level of light interception at different developmental stages. Futhermore, maintaining high levels of SLA may involve greater leaf area duration and less falling leaves. Higher SLA also could lead to a reduction in photosynthetic apparatus per unit leaf area. However, a larger leaf area might increase canopy light interception, and thus, compensates for a CO_2 assimilation reduction (Richards, 2000). In the case of cultivars of Arracacha studied under field conditions, A_n and A_{tot} were higher with high SLA. These agree with those reported by Mediavilla et al. (2001) for several woody species. Additionally, SLA was positively associated with relative growth rate in other crops (Lambers et al., 1998). Consequently, the possibility exists for increasing assimilates partitioning to storage roots, especially during the last stage of root growth. Similar results were also reported by El-Sharkawy (2006a) for cassava where a linear relationship existed between final dry root-yield and seasonal leaf area index for 30 clones. Pineda (1988) found that a greater reduction in leaf area occurred at 300 dap in Arracacha cultivars coinciding with higher dry root weight and probably related to with leaf fall.

The significant relationships between A_n, A_{max}, A_{tot} and root-yield indicate that it is possible to select cultivars of *A. xanthorriza* for high productivity using these variables as physiological indicators for high root-yield. It seems that for *A. xanthorriza* a higher A_n implies greater allocation of assimilates towards the roots in absence of alternative sinks. El-Sharkawy (2004) and El-Sharkawy et al. (1990) reported that CO_2 assimilation can limit root-yield in field-grown cassava in crop canopies where light interception is not a limiting factor (i.e. high seasonal leaf area index and leaf area duration), however, more studies and research is needed to confirm this in Arracacha. The average of CO_2 assimilation during the life cycle of five cultivars of *A. xanthorrhiza* are low for a root crop grown at hight altitude. For example, by screening large cassava accessions (field-grown at 1800 m a.s.l., with mean annual temperature of 17–18 °C), El-Sharkawy (2006a) reported CO_2 assimilation rates between 16 and 17 μmol CO_2 m^{-2} s^{-1}. These rates were mainly attributed to nonstomatal factors (i.e., biochemical/anatomical leaf traits).

These findings indicate the importance of including leaf photosynthesis, as a selection criterion, in breeding cultivars adapted to different environments. The observed genotypic variations in CO_2 assimilation rates in Arracacha under different environments, which can be fundamentally associated to micro-climatic conditions, must be further investigated using larger accessions. Identification of genotypes with high leaf photosynthesis could be included in breeding programs for developing best adapted new cultivars with higher yields for a specific environment.

Root-yields found in this work were higher than those reported for the Capuri area, where yield are 1.6 and 1.5 kg m^{-2} of commercial root for Cha and Cb,respectively (Noguera, 2001). In Santa Rosa, Briceño (1975) obtained similar results with densities of 1.0 m × 0.6 m. The national average yield is 1.2 kg m^{-2} (MAC, 1996). Añez et al. (2001), under experimental conditions using different spacings report higher production with greater densities with the largest yields of 2.9 kg m^{-2} obtained for the Cha cultivar.

In conclusion, the most productive cultivars in the current experiment were Ban, Cb and Cha in Capuri and Cb and Cha in Santa Rosa, as they had the highest values of A_n, A_{max}, A_{tot}, and SLA. These parameters could be used as indicators of high root productivity when selecting cultivars of *A. xanthorriza*. Further studies are still needed on the relationship between A_n and the patterns of distribution of assimilates within plant organs. As shown with our results in the present study, higher A_n, A_{max} and A_{tot} might imply a greater transport of assimilates towards the roots. This may also depend on varying soil, nutrients, water and light conditions.

Acknowledgements

This research was financed by CDCHT (project no. FO-572-05-01 B) Universidad de los Andes, Merida Venezuela. We wish to thanks to M.A. El- Sharkawy for his helpful comments and editing of the manuscript. We are grateful to Gerardo Maggiorani at Capuri for the logistic support

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