NAA and STS effects on bract survival time, carbohydrate content, respiration rate and carbohydrate balance of potted *Bougainvillea spectabilis* Willd.

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Abstract

The aims of this work were to deepen the knowledge on the physiology of bract abscission in *Bougainvillea spectabilis* 'Killie Campbell' plants, in what relates to respiration and carbon balance. Using the effects induced by Silver Thiosulphate (STS) and/or Naphtalene Acetic Acid (NAA, at high concentration: 500 $mg.l^{-1}$) on bract abscission under interior conditions, the relationship between bract survival time (longevity) and, respiration rate or carbohydrate levels, was investigated.

Treatments that included NAA were the ones that reduced significantly bract abscission. Unexpectedly, the higher the levels of bract soluble and total carbohydrates, measured at day 10 postproduction (PP), the higher the abscission of bracts. These results show, for the first time, that abscission can positively correlate with non structural carbohydrates levels in the organ that abscise.

Bract respiration rate was significantly affected by treatment and postproduction day (PP). Treatments that had higher bract respiration rates (WATER and STS) also had higher levels of non structural carbohydrates in the bracts. Bract respiration rate decreased from day 10 to day 17 PP by approximately 50% (on average of all treatments) and was negatively correlated with bract survival time.

In the carbon balance per gram of bract dry weight, the treatments WATER and STS, showed the largest decrease in the content of total carbohydrates and had the highest consumption of carbohydrates through respiration. So, these were the bracts that needed to import a higher amount of carbohydrates per gram of bract dry weight. In the carbon balance for the whole mass of bracts and adjacent stems in an average plant, the treatments WATER and STS continued to allow for the largest decreases in total carbohydrate during postproduction. However, and contradicting the results per gram of bract dry weight, the highest total consumption of carbohydrates by respiration was obtained for the NAA and STS+NAA treatments. It makes sense that bracts that last longer have lower individual carbon consumption while, at the plant level, the increased number of remaining bracts causes a higher overall expenditure.

Respiration rate has been used as an indicator of flower longevity, this correlation is here extended for the flower+bract system. Plants that had higher bract respiration rates, most probably, had a higher flow of carbohydrates through the bracts (and flowers), which, in the end, was sensed as a higher carbohydrate level.

Keywords: Ornamentals; Postproduction; Postharvest; Auxin; Longevity; Keeping quality.

1. Introduction

Flower/bract drop in potted plants is a major problem leading to losses of quality and, as consequence, loss of market value. The ability to control/predict flower/bract abscission and enhance longevity of floricultural product is of great importance.

The abscission process is controlled by both external environmental conditions and internal (genetically controlled development time and, energy availability) mechanisms (Ascough *et al*., 2005). The respiration rate is considered a good indicator of longevity, correlating negatively with organ longevity (Reid, 1985). In potted chrysanthemum, cultivars with higher flower respiration rate during postproduction had shorter flower longevities under interior conditions (Monteiro, 1991). Similar results were obtained in potted miniature roses in the summer experiments but, the opposite happened in autumn/winter: flowers with higher respiration rates had greater longevities. It seems that environmental conditions imposed stringent restrictions on the respiration of the flowers and, on the energy available for its development, the limiting factor to their longevity (Monteiro, 1993). A low maintenance respiration may be responsible for higher levels of efficiency at low irradiance, as was observed in *Brassaia actinophylla* Endl., *Nephrolepis exaltata* (L.) Schott 'Bostoniensis' and *Epipremnum aureum* (Linden & Andre) (Pass and Hartley, 1979). Respiration rate may also sense the speed of genetically controlled development both in plants (Pearl, 1928) and in animals (Adelman *et al.*, 1988).

In the postproduction of flowering potted plants the main stress is low irradiance, either acting through hormone mediated responses or, directly, through negative net photosynthesis. Also, it is known that considerable amounts of carbohydrates are necessary for the development/maintenance of the reproductive organs (Ho and Nichols, 1977; van Meeteren *et al.*, 1995; Waithaka *et al.*, 2001). The levels existing in these organs as well as the amounts that can be obtained from other plant parts (or exogenous

77 supply) seem to affect flower/bract longevity.

78 Several positive correlations have been established between carbohydrates levels
79 and flower longevity, as in chrysanthemum (Monteiro, 1991), Christmas begonia (Fjeld,
80 1992) and asiatic hybrid lily tepals (detached flowers) (van der Meulen-Muisers *et al.*,
81 2001). *Lilium* L. ('Bright Beauty', 'Fashion' and 'Orlito') flower longevity relies on the
82 carbohydrates translocated from other plant parts (van der Meulen-Muisers *et al.,* 2001).
83 An exogenous supply of carbohydrates delays abscission, or flower wilting, prolonging
84 the longevity of some cut flowers like *Strelitzia reginae* Ait. (Halevy *et al.*, 1978),
85 carnation (Halevy and Mayak, 1979), *Delphinium* hybrid 'Bellamosum' (Ichimura *et*
86 *al.*, 2000) and *Alstroemeria ´*Rebecca' (Chanasut *et al.*, 2003). The same effect was
87 described for potted miniature rose (*Rosa hybrida* 'Meijikatar') flowers (Monteiro *et al.*,
88 2002). However, there are species in which the exogenous supply of carbohydrates does
89 not extend the life of flowers like hybrid *Limonium* (Ichimura, 1998), *Celosia argentea*
90 L. 'Forest Fire' and *Helianthus maximilianii* Schräd (Redman *et al.*, 2002).

91 Ethylene and auxins have been involved in the abscission process. Two abscission
92 processes of floral organs have been shown: one ethylene dependent and the other
93 ethylene independent (Patterson and Bleecker, 2004). Ethylene seems to enhance
94 respiration rate in flowers, and commonly hastens the process of senescence and/or
95 abscission (Woltering, 1987; Borochov and Woodson, 1989). STS acts as an ethylene
96 inhibitor (sensing and action) (Veen, 1979; Reid, 1985) thus, counteracting ethylene
97 action.

98 The role of auxins seems less clear: they affect ethylene sensitivity and production
99 (Beyer and Morgan, 1971; McManus *et al.*, 1998; Brown, 1997) and carbohydrate
100 partitioning (Zhao and Oosterhuis, 1998; Nahar and Ikeda, 2002). In tomato, auxin may
101 be responsible for a higher carbohydrate supply to early developing flower tissue (Pröls,

2004). Auxin direct effect on respiration is rarely mentioned. Sacalis and Nichols (1980) showed that the effect of the auxin 2,4-D on the respiration rate of carnation flower, depended on the concentration applied. Compared to water controls, CO_2 production was accelerated by uptake of 4, 20 and 100 mg of 2,4-D.l^{-1}. However, 500 mg 2,4-D.l^{-1} suppressed CO_2 and ethylene evolution and retarded senescence. In small fruits, some studies involving auxin application (15, 25 or 50 mg NAA.l^{-1}), have shown a reduction in dark respiration in the tissues of developing apples (Stopar *et al*., 2001) and medlar (Amorós *et al*., 2004). In the whole plant level, depending on the dose and time of application, auxins can either induce abscission or counteract it in citrus fruits (Greenberg *et al.*, 2006; Gupta and Kaur, 2007; Yuan and Carbaugh, 2007).

In young excised bougainvillea ('Purple Flower' and ´Taipei Red') bracts, Chang and Chen (2001) reported ethylene production. Also, Xin and Lin (2005) showed a climacteric ethylene production pattern in *B. glabra* and *B. spectabilis* during flower opening and senescence. However, for *B. spectabilis* 'Killie Campbell', in the absence of exogenous ethylene, STS alone is not very effective on counteracting bract abscission (Gago *et al.*, 2001; Meir *et al*., 2007) while NAA (500 ppm), at end of production, substantially reduces bract abscission under interior conditions. In the presence of exogenous ethylene, both STS and NAA are needed to control effectively bract abscission (Gago *et al.*, 2001). The auxin 2, 4, 5-TP, was shown to have the same effect as NAA (Meir *et al.*, 2007).

Thus, it seems probable that in bougainvillea under interior conditions, the abscission process can be related to respiration rate and/or carbohydrate levels. Regardless of the primary control of bract abscission (ethylene dependent or independent), the knowledge of how it proceeds may help us devise strategies for its control. The objective of this work is to deepen the knowledge on the physiology of

bougainvillea bract abscission, in what relates to respiration and carbon balance. Using the variability induced by STS and/or NAA treatments, the respiration and carbohydrate levels were assessed in several plant parts, to try to establish correlations with bract abscission and to compute some simplified carbohydrate balances.

2. Materials and methods

2.1. General procedures

Two postproduction experiments with *Bougainvillea spectabilis* 'Killie Campbell' plants were done (beginning at: June 20, 2002 - experiment one, and August 25, 2003 - experiment two), with completely randomized designs and five replications per treatment.

Plants were grown in plastic greenhouses, using the normal procedures, at the "Horto" of University of Algarve, Faro, until the beginning of the experiments. The only environmental control provided was greenhouse ventilation when temperature exceeded 24 ºC. Temperature was monitored hourly with a temperature logger (Testostor 175, Testo GmbH & Co., Lenzkirch, Germany). On both experiments, at the beginning of the plant production period, i.e. the winter months (December/January) the minimum temperature went down to 6ºC and the maximum temperature rose to 21ºC. At the end of the production period (June/August) temperature ranged from a minimum of 20ºC to a maximum of 35ºC.

At end of production, plants had approximately 60 cm height, at least ten bracts completely developed and, at least one of them with an open flower (at anthesis). The term bract, unless mentioned otherwise, refers to the bracts + flowers, i.e. an inflorescence with 3 flowers and 3 bracts.

153 Treatments with STS were initiated during production, starting when bracts
154 became visible, and were applied every 15 days up to end of production. They consisted
155 of a 160 mg.l^{-1} spray of STS (2 g.l^{-1} of Argylene®; Argylene Biochem ApS,
156 Frederiksberg, Denmark). Treatments with NAA consisted of a single spray, at the end
157 of production (day 0 postproduction), using 500 mg.l^{-1} of NAA (30.30 g.l^{-1} of
158 Agritone® (0.45%NAA+1.2%NAA-amide; Etisa, Barcelona, Espanha)). Both types of
159 spray were done to wet uniformly the leaves and bracts, up to start of dripping.
160 Treatments performed were: a) STS, b) NAA, c) STS+NAA and d) WATER.
161 Once dry from the sprays, plants were sleeved, boxed in open card boxes - 10
162 plants per 30×52×50cm (height X length X width) box, and kept for three days under
163 simulated transport conditions (17±1ºC, no light).
164 At day 3 postproduction (PP) plants were unboxed, removed from the sleeves and
165 placed under interior conditions [21±1ºC and 12 μmol.m^{-2}.s^{-1} of cool white fluorescent
166 light (Philips,TLD, 58/830) 12 hr a day].
167 At end of production (day 0 PP), end of simulated shipping (day 3 PP) and, twice
168 a week, through the remaining of postproduction, the number of bracts remaining in the
169 plants was assessed (all bracts stages)
170
171
172 **2.2. Respiration measurement**
173
174 At day 10 and day 17 PP, the measurement of dark respiration was made
175 separately for two plant parts: a) bracts: all the bracts and the small stems that support
176 them on each plant (TBS), b) leaves: all the leaves existing in the 20 cm of stem below
177 the bract zone and the respective small stems (TLS).

178 CO_2-exchange measurements were made in a closed system, using an IRGA
179 (model CI-301 (CI-301PS) CID Inc., Vancouver, WA 98682 USA) equipped with a 4
180 liters chamber. Attached bracts or leaves were conveniently enclosed in the chamber
181 and the chamber was flushed with outside air to bring the CO_2 levels to approximately
182 360 ppm. The system was then changed to a closed circuit and the measurements done
183 in absolute mode. Ten consecutive measurements at 25 s intervals were taken for the
184 rate of CO_2 increment, and the average of these measurements recorded.
185 Bracts, stems adjacent to the bracts, leaves and stems adjacent to the leaves, were
186 harvested separately, dried and their dry weight (DW) assessed. Bract + adjacent stem
187 respiration rate (BS) and leaf + adjacent stem respiration rate (LS) were expressed per
188 gram of bract and leaf dry weight, respectively.
189
190 **2.3. Carbohydrate assessment**
191
192 At days 10 and 17 PP, after 4 hours of exposure to light, samples for bracts, leaves
193 and stems were taken separately. Samples consisted of: a) bracts: all the bracts existing
194 in the plant, b) leaves: all the leaves existing in the 20 cm of stem below the bract zone,
195 c) stems: the 20 cm of stem below the bract zone, where the leaves were previously
196 harvested.
197 Some plants sprayed with WATER and STS lost all the bracts before day 10 and
198 day 17 PP, respectively, reducing the number of replications.
199 All fresh plant material was weighed and immediately frozen in liquid nitrogen,
200 being then dried in a ventilated oven at 80ºC. When completely dry, they were ground
201 in a mill (MF 10 basic, IKA ®, Werke) and then re-dried in the same oven for a short
202 period. After proper homogenization, a 0.1g sub-sample for each plant part was used for

carbohydrate extraction. Total non structural carbohydrates were assessed (soluble sugars and starch separately) using the phenol-sulphuric method (Dubois *et al.*, 1956) following the procedure described by Stamps (1984).

2.4. Calculations

2.4.1. Bract respiration

Due to the way respiration was measured, it was not possible to separate, directly, bract respiration, from respiration of the adjacent stem. To allow for this separation, a linear model was used:

TBS=**a**+Bdw×**br**+Sdw×**sr**+**t**×DPP

TBS – total respiration in bracts + adjacent stems (mg $CO_2.h^{-1}$)

a - constant

Bdw – bract dry weight (g)

br – bract respiration (mg $CO_2.g^{-1}$ bract dry weight.h^{-1})

Sdw – stem dry weight (g)

sr – stem respiration (mg $CO_2.g^{-1}$ stem dry weight.h^{-1})

t – change in respiration rate per day (mg $CO_2.day^{-1}.h^{-1}$)

DPP – day postproduction for the measurement

2.4.2. Carbon balance

A simplified carbon balance was computed using respiration and carbohydrate data. For that purpose it was assumed: (1) that the plants, or their organs, did not photosynthesize (either in the complete dark or with the low light intensities of 12

228 μmol.m^{-2}.s^{-1}) during PP (no published information exists on bougainvillea
229 photosynthesis at low irradiances) and, (2) that respiration rate was constant through the
230 whole 24 hr period (i.e. during the dark or the low light intensity period). Mean daily
231 respiration was considered as the average of day 10 and day 17 PP.
232 For the different treatments, three different types of carbon balance were calculated,
233 between day 10 and day 17 PP, as shown in Table 1.
234
235 **2.5. Statistical analysis**
236 Bract abscission data was analyzed using survival analysis (Kleinbaum and Klein,
237 1995).The survival time started at the beginning of the postproduction period and ended
238 when bract abscission was observed. An observation was censored when the bract was
239 still on the plant by the end of the experiment. Survival times were analyzed using the
240 Kaplan-Meier technique (Kleinbaum and Klein, 1995), producing the empirical survival
241 curves for the four postproduction treatments. The difference in survival times between
242 the treatments were tested with the log-rank test. A disadvantage of this method is that
243 the effects of the explanatory factors (covariates) cannot be quantified (Wubs et al.,
244 2007*)*.
245 For carbohydrate levels and respiration rate a 3-way factorial was used
246 (experiment × day PP × treatment). When needed, means were compared using
247 Duncan's New Multiple Range Test at *P*=0.05. Linear regressions were also run when
248 appropriate. Softwares used for the statistical treatments were SAS (SAS Institute
249 Inc.,Cary, NC,USA) and SPSS (SPSS Inc., Chicago, USA).
250
251
252 **3. Results**

253

254 **3.1. Bracts survival time**

255

256 Plants sprayed with NAA and STS+NAA did not differ in their bracts' survival
257 time (29.57 and 29.85 days, respectively; at P=0.997), but had a significantly higher
258 survival time than bracts treated with WATER or STS (at P<0.0001). Bracts sprayed
259 with STS survived longer (11.18 days) than bracts sprayed with WATER (10.11 days;
260 at P<0.0001). Bracts treated with WATER and STS abscised more intensively in the
261 first 11 days of postproduction period. In that period, plants treated with STS and
262 WATER had similar fractions of surviving bracts. At day 15 PP, plants treated with
263 WATER or STS had less than 5% or 15% of surviving bracts, respectively. On the same
264 PP day, plants sprayed with NAA or STS+NAA had more than 80% of surviving bracts
265 (Fig. 1).

266

267

268 **3.2. Carbohydrates**

269

270 *Bracts*

271 Bract carbohydrate levels (starch, soluble and total carbohydrates) were significantly
272 affected by PP treatments (at P=0.022, P=0.0001 and P=0.0001, respectively) and the
273 PP day (at P=0.0431, P=0.0001 and P=0.0001, respectively). The levels of soluble and
274 total carbohydrates were also affected by experiment (at P=0.0210 and P=0.0172,
275 respectively), with the higher values in the 2003 experiment. Since bract starch and total
276 carbohydrates presented an interaction between treatment and PP day, data are
277 presented by treatment and PP day for all types of carbohydrates assessed (Fig. 2). On

278 day 10 PP, bracts sprayed with STS and WATER had the highest levels of total
279 carbohydrates, while the differences among treatments in soluble carbohydrates and
280 starch were less marked. At day 17 PP, STS treated bracts still had the highest soluble
281 and total carbohydrates levels, but WATER treated bracts had levels similar to the
282 bracts sprayed with NAA or STS+NAA. At this time bract starch content was similar in
283 all treatments. Between days 10 and 17 PP, bracts sprayed with WATER and
284 STS+NAA reduced the content of soluble (at P=0.0123 and P=0.0041, respectively)
285 and total carbohydrates (at P=0.0083 and P=0.0025, respectively) and, only bracts
286 treated with STS reduced the level of starch (at P=0.0151).
287 The higher the levels of soluble and total carbohydrates (Fig. 3), measured at day
288 10 PP, the shorter the bract survival time. However, the higher the percentage of starch
289 in the bracts, measured at day 17 PP, the longer the bracts survive (Fig. 3).
290
291 *Leaves*
292 Leaf soluble and total carbohydrate levels were significantly affected by an
293 interaction between treatments and experiments: in 2002, no differences were found
294 among the levels of carbohydrates (soluble and total) of the different treatments (Fig. 4
295 A), while in 2003, plants sprayed with WATER and NAA presented higher levels of
296 leaf soluble and total carbohydrates (Fig. 4 B).
297 Experiment affected the levels of soluble sugars (at P=0.001), total non structural
298 carbohydrates (at P=0.001) and percentage of starch (at P=0.0198).
299 Day of carbohydrate assessment (i.e. day PP) affected the levels of starch, soluble
300 carbohydrates and starch percentage on leaves, independently from treatment and
301 experiment. The starch content at day 10 PP (17 mg glucose.g^{-1}DW) was higher than at
302 day 17 PP (9 mg glucose.g^{-1}DW). The reverse happened with the soluble carbohydrates

having 33 mg glucose.g^{-1}DW, at day 10 PP, and 36 mg glucose.g^{-1}DW, at day 17 PP. Total carbohydrates did not differ between days 10 and 17 PP, but the percentage of starch in leaves decreased from 25% to 20% (at P=0,0119). No effect of treatment or experiment could be found in the levels of leaf starch. Also, the percentage of starch in leaves was not affected by postproduction treatment but was affected by the experiment. Overall, the percentage of starch (average of the 4 postproduction treatments) was higher in the plants of the 2002 experiment (24.4%) than in plants of the 2003 experiment (20.64%). No correlations were found between the levels of leaf non structural carbohydrates and bract abscission.

3.3. Respiration

3.3.1. Bracts

Bract respiration rate (BS) was significantly affected by treatment and day PP (at *P*=0.0074 and *P*=0.0011, respectively). Plants sprayed with WATER presented the highest bract respiration rate, followed by intermediate values on plants treated with STS and STS+NAA and, the lowest respiration rates occurred on bracts sprayed with NAA (Fig. 5 A).

Respiration rate decreased from day 10 to day 17 PP (Fig. 5 B) by approximately 50% (on average of all treatments).

Separation of bract from stem respiration

At all postproduction treatments TBS was reasonably explained by bract and stem dry weights and by postproduction day (Table 2). Estimated bract respiration rate (**br**) presented slightly lower values in plants sprayed with NAA. Also, stem respiration rate

328 (**sr**) presented lower values in plants treated with NAA but, these values were very close
329 to the values computed for WATER, STS and STS+NAA treatments. In all
330 postproduction treatments **sr** was lower than **br**: less than 50% in WATER, NAA and
331 STS. Only in STS+NAA, **sr** was about 70% of **br** (Table 2).
332 When compared to the WATER control, STS alone lowered the model constant
333 (**a**) and, the treatments with NAA (with or without STS) presented the highest values.
334 Similar results were obtained for **t,** the decrease of respiration rate by day PP.
335
336
337 *Relationship between bract respiration and bract survival time (longevity)*
338 Bract respiration, as measured together with the adjacent stems (BS) on days 10
339 and 17 PP, or estimated (**br**), negatively correlated with bract longevity. However, it
340 was BS at day 17 PP, who showed the best correlation (Fig. 6).
341
342 *Relationship between bract respiration and carbohydrate levels*
343 Using the carbohydrate data and pooling the data for the two experiments, and for
344 days 10 and 17 PP, the treatments that had a higher estimated bract respiration rate (**br**)
345 were those with more non structural carbohydrates in the bracts: starch, soluble and
346 total (Fig. 7).
347
348 *Bract carbon balance*
349 Considering the carbon balance per gram of bract dry weight (**br**), the treatments
350 WATER and STS, showed the largest decrease in the content of total carbohydrates and
351 had the highest consumption of carbohydrates through respiration (Table 3). So, these
352 were the bracts that imported an higher amount of carbohydrates per gram of dry

353 weight. Plants treated with NAA or STS+NAA presented similar values of **br**, but the
354 decrease in total carbohydrates was higher in the STS+NAA treatment.
355
356 In the carbon balance for the whole mass of bracts and adjacent stems in an
357 average plant (Table 4), the treatments WATER and STS continued to allow for the
358 largest decreases in total carbohydrate. However, and contradicting the results per gram
359 of bract DW, the highest total consumption of carbohydrates by respiration appeared in
360 the NAA and STS+NAA treatments. Most probably, the more bracts remained in a
361 plant, the greater the expenditure of carbohydrates. Indeed, between days 10 and 17 PP,
362 in the plants treated with WATER and STS, bract dry weight was only 40% of the
363 whole mass of bracts and adjacent stems, whereas in the NAA and STS+NAA
364 treatments, bracts represented about 60%.
365
366 **3.3.2. Leaf**
367
368 The respiration rate in leaves + adjacent stem (LS), in the dark, was not affected
369 by postproduction treatment, but was significantly influenced by experiment (at
370 P=0.0025) and by postproduction day (at P=0.0107), and there was an interaction
371 between these two effects (at P=0.0503).
372 All treatments decreased their LS from day 10 to day 17 PP (data not shown). No
373 correlations could be established between the abscission of leaves (data not shown) and
374 their respiration rate. Variability was considerable. Also, leaf respiration was measured
375 in the upper part of the plant (the 20 cm of stem below the area of bracts), while the
376 leaves that fell the most, were in the lower part.

In the 2003 experiment, at day 17 PP, a higher LS, was related to a lower level of leaf total carbohydrates, on that day [LS = 2.197 – 0.0309 × total carbohydrates (mg glucose.g^{-1} leaf DW); R^2=0.893 e *P*=0.0552]. However, it was not possible to establish this correlation for 2002.

The carbon balance of the whole mass of leaves assessed and their adjacent stems was performed (Table 5) for the two experiments. More than differences among treatments there were differences between experiments (data not shown). In 2002, the decrease in the content of total carbohydrates, from day 10 to day 17 PP was high and superior to the respiration needs, leading to some export. In 2003, comparing with 2002, there was a higher consumption by respiration, and a smaller decrease in the carbohydrate content of the leaves, leading to a computed import of carbohydrates.

These results suggest that the different treatments did not influence substantially the carbon balance in the leaves, and may suggest that the plants in the two experiments had different leaf age. Unfortunately, photosynthetic rates were not measured and it is unknown if it had any role in the balance. Percent of dry weight of leaves in the total weight of leaves and adjacent stems differed with experiment: 52% in 2002 and 30% in 2003.

4. Discussion

In this work, the pattern of bract abscission obtained by STS and/or NAA treatments was similar to the results presented by Gago *et al.* (2001). Clearly the treatments that prolong bract survival time or, what is the same, reduce bract abscission (Fig.1) are the ones that include NAA.

In bougainvillea bracts, the content of soluble sugars was always much higher than the starch content (Fig. 2), suggesting that these are places of transit or consumption of carbohydrates. Previously, Zhao and Oosterhuis (2000) showed the importance of cotton bracts in the adjustment of the transport of photoassimilates to the flower parts. To determine whether bougainvillea bracts have or not a function on carbohydrates supply to the flower, bract and flower carbohydrates should have been quantified separately, which unfortunately was not done.

As it was expected, STS and/or NAA treatments induced variability in the carbohydrate levels of several plant parts. It was possible to establish correlations between bract abscission rate and carbohydrate levels in some plant parts (bracts and stems (data not shown)), however, in an unexpected way. Bracts which showed higher contents of soluble and total sugars, initially, were those that had the lowest longevity (Fig. 3). These results differ from those presented so far in the literature, where examples exist of positive correlations between the levels of flower non structural carbohydrates and its longevity as well as of negative correlations between the carbohydrate content of an organ and its abscission. Begonia inflorescences with higher contents of sucrose and starch had greater longevities (Fjeld, 1992). The stress caused by low light intensities (80% reduction in light level) influenced the photoassimilates availability to flower/fruit development in pepper: cultivars with higher flower and/or fruit abscission had lower content of non structural carbohydrates (Wien *et al*, 1989).

Bracts have intermediate characteristics between leaves and petals and little research has been done on these plant organs. In this study, when referring to bracts, flowers are also included, and it is unknown in bougainvillea, despite their abscission as a whole, to what extent these two organs behave in a similar way. As far as carbohydrate levels and abscission are concerned, these two organs may have different

427 physiologies, and the different dry weights or different carbohydrate levels, may mask
428 the individual effects. Nevertheless, whatever the prevalence is, these results show, for
429 the first time that longevity can negatively correlate with non structural carbohydrates
430 levels in the organ. However, bracts with higher percentages of starch, at day 17 PP, had
431 lower abscission rates (Fig. 3). An increased starch percentage may mean that there is
432 'excess' of carbohydrates (as of higher transit, higher import, and/or lower
433 consumption) in a sink organ as we assume bracts to be. An higher priority for storage,
434 is also possible in a source or storage organ.

435 The carbohydrates content may not be a reliable estimate of their availability: it
436 does not reflect the rate of utilization, the proportion that is not available or the rate of
437 import from other plant parts. An higher content of soluble sugars (or total
438 carbohydrates) may have different explanations such as: an higher rate of
439 import/production for a reduced or constant consumption; a constant rate of
440 import/production together with a lower consumption,... Nevertheless, a more active
441 metabolism, with an higher rate of consumption and an higher rate of
442 import/production, i.e. an higher flow of carbohydrates through the organ, may also be
443 sensed as an actual, higher content of carbohydrates.

444 Both bract and leaf respiration rate decreased, between days 10 and 17 PP. This
445 decline in respiration rate may be due to a lack of carbohydrates available or, a
446 reduction in metabolic activity. Decreases in respiration rate (decreased metabolic
447 activity) induced by low irradiance have been shown in leaves (Noguchi *et al.*, 2001),
448 where this decrease is essential to maintain a positive (or less negative) balance of
449 carbohydrates. Inflorescence/flower respiration under interior conditions is also known
450 to decrease during postproduction, as it was reported for chrysanthemum (Monteiro,
451 1991). No previous information, specific for bracts under interior conditions, exists.

However, according to what is known for flowers and leaves, the decrease in bract respiration rate was expected.

Bract respiration rate (**br** as estimated or BS as assessed) negatively correlated with bract survival time. In general biology, it is common that species or organs with higher respiratory rates have shorter longevities (Cevallos and Reid, 2000) and respiration rate has been suggested as an indicator of flower longevity (Kuc and Workman, 1964; Reid, 1985; Monteiro, 1991). Here, this correlation is extended for the flower+bract system.

This study is consistent with previous works in which respiration rate is negatively correlated with the longevity of the floral organs (Monteiro, 1991; Monteiro, 1993; Grossi *et al.*, 2003). In the previous studies, the causes of variation that influenced the respiratory rates were often the genetic differences (different cultivars), treatments that directly affect the speed of chemical reactions (such as temperature), or substances such as STS that prevent ethylene action. Here, for the first time, it is shown that the effect of NAA, in the maintenance of bracts of plants kept at low irradiance, is accompanied by a decrease in the respiratory rate per gram of brac. This type of response was previously found in apple (Stopar *et al.*, 2001) and medlar growing fruits (Amorós *et al.*, 2004).

The meaning of the positive correlation between bract respiration rate and carbohydrate level in the bracts is not so clear. We expected carbohydrate levels to be lower in the treatments where their consumption was higher and the opposite happened. It is possible that, if carbohydrate availability was a limiting factor, higher amounts of available carbohydrates in the bracts allowed for higher respiration rates. However, it does not make much sense that increased carbohydrate availability (although inducing increased respiration rate) goes together with shorter bract longevity. In potted

477 miniature roses (Monteiro *et al.*, 2001), when a lack of carbohydrate availability existed,
478 flower longevity decreased and if the limitation was overcome, the flower respiration
479 rate increased simultaneously with flower longevity. We are more prone to the
480 hypothesis that, in the plants that had higher bract respiration rates, there was an higher
481 flow of carbohydrates through the bracts (and flowers), which, in the end, was sensed as
482 an higher carbohydrate level.

483 Rather interesting are the completely different results found in the two carbon
484 balances performed: a) per gram of bract dry weight and b) for the whole mass of bracts
485 plus adjacent stems in the average plant. Comparing the treatments with delayed bract
486 abscission (the ones including NAA) with the others: in the balances per gram of bract
487 dry weight, the former had the lowest carbon consumptions, while in the balances for
488 the whole mass of bracts and adjacent stems in the average plant, these same treatments
489 had the highest carbon consumptions. These differences were mainly due to the higher
490 number of bracts present in the plants during the postproduction period. It makes sense
491 that bracts that last longer have lower individual carbon consumption while, at the plant
492 level, the increased number of bracts remaining in the plant, causes a higher overall
493 expenditure. It is clear that treatments allowing for longer bract persistence are the ones
494 that, in a whole plant basis, spend more carbon for overall floral organ maintenance.
495 This is in accordance with the lower levels of starch found in the stems (data not shown)
496 of plants from the treatments with NAA, strengthening the hypothesis that
497 bracts+flowers are mainly places of consumption.

498 Plants sprayed with NAA had modified carbon partitioning rates to the bracts. The
499 importance of the carbohydrate levels for the control of bract abscission in
500 bougainvillea is still unknown. Nevertheless, recent works have been stressing the
501 importance of some carbohydrate molecules (mainly glucose), interacting with plant

hormones (ABA, auxin, ethylene, ...) in the regulation of plant growth and development (Sheen, 2010).

No differences in respiratory rates of leaves, induced by postproduction treatments were detected but, plants of the two experiments seemed to be in different stages of their development. In 2002, the leaves may have provided energy for development and maintenance of bracts, which did not seem to happen in 2003 (Table 5). Probably, these differences may be associated with differences in leaf age and/or different conditions of plant production: Stahl and McCree (1988) reported that in *Sorghum bicolor*, the two components of respiration in the dark, maintenance respiration and growth respiration decrease with age of the leaf.

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647
648

Table

Table 1 – Carbon balance calculations, for the different treatments, between day 10 and day 17 PP: (a) per gram of bract dry weight (using the estimate of bract respiration, br), (b) for the whole mass of bracts and adjacent stems existing in the average plant (using measured values, TBS), (c) for the whole mass of leaves and stems in the 20 cm below the bract zone, for the average plant (using measured values, TLS).

Assessment	Calculation
Variation in carbohydrate levels from day 10 PP to day 17 PP	Δ Total carbohydrates (mg glucose) *= Total carbohydrates at day 17* - Total carbohydrates at day 10*
Carbohydrate consumption through respiration for the 7 day period	Total consumption of carbohydrates (mg glucose)*=(R**×24 h×7 days)/1.47
Imported carbohydrates, calculated from the consumption of carbohydrates and the variation of carbohydrates levels between day 10 and 17 PP	Total carbohydrate import *(mg glucose) = Total consumption of carbohydrates + Δ Total carbohydrates
Daily carbohydrate import	Daily import carbohydrates*(mg glucose.day^{-1}) = Total carbohydrate import/7 days

*on bracts (a), expressed on mg glucose per gram of bract dry weight;
on bracts + adjacent stems (b), expressed on mg glucose for the average plant;
on total leaves + adjacent stem in the 20 cm below bracts (c), expressed on mg glucose for the average plant.
**(a) R= br; (b) R= TBS; (c) R= TLS

Table

Table 2 – Linear model TBR= **a**+Bdw×**br**+Sdw×**sr**+**t**×DPP, for each postproduction treatment: significance level (*P*), determination coefficient (R^2) and estimated parameters (**a**, **br**, **sr** and **t**). Each value was obtained using data from the two experiments.

	Postproduction treatments			
	WATER	STS	NAA	STS+NAA
P	0.0002	0.0008	0.0016	0.0012
R^2	0.8778	0.7135	0.6530	0.6687
a	1.2384	0.4374	1.4728	1.885
br[*1]	0.6539	0.8815	0.3456	0.3552
sr[*2]	0.2370	0.2906	0.0168	0.2486
t[*3]	-0.0787	-0.0335	-0.0824	-0.1142

[1] mg $CO_2.h^{-1}.g^{-1}$ bract DW,[2] mg $CO_2.h^{-1}.g^{-1}$ stem DW, *[3] mg $CO_2.day^{-1}.h^{-1}$

Table

Table 3 – Different treatments carbon balance, between days 10 and 17 PP, per gram of bract dry weight. The balance was computed using data from the 2002 and 2003 experiments. Bract respiration rate (**br**) was estimated from assessed values of bract+adjacent stem respiration rates.

Carbon balance -per g of bract dry weight-					
Postproduction treatment	$\Delta total_B$*	**br****	Total consumption by **br***	Total import*	Daily import***
WATER	-22.120	0.446	74.885	52.765	7.538
STS	-10.131	0.601	100.949	90.819	12.974
NAA	-3.294	0.236	39.578	36.284	5.183
STS+NAA	-8.291	0.242	40.677	32.386	4.627

$\Delta Total_B$=Variation in bract carbohydrate levels
*(mg glucose.g^{-1} bract dry weight);
**(mg glucose.g^{-1} bract dry weight. h^{-1});
*** (mg glucose.g^{-1} bract dry weight.day^{-1}).

Table

Table 4 – Different treatments carbon balance, between day 10 and 17 PP, for the whole mass of bracts and adjacent stems of an average plant. The balance was computed using data from the 2002 and 2003 experiments.

Carbon balance, whole mass of bracts and adjacent stems, in an average plant - Postproduction treatments	$\Delta Total_{B+S}$*	TBS**	Total consumption by TBS*	Total import*	Daily import***
WATER	-40.350	0.455	76.512	36.162	5.166
STS	-22.636	0.390	65.591	42.955	6.136
NAA	-5.609	0.541	90.912	85.303	12.186
STS+NAA	-10.639	0.636	106.838	96.198	13.743

$\Delta Total_{B+S}$ = Variation in the bract+adjacent stem carbohydrate levels; TBS= total (bract+ adjacent stems) respiration rate.
*(mg glucose. average plant^{-1});
**(mg glucose. average plant^{-1}. h^{-1});
*** (mg glucose. average plant^{-1}.day^{-1}).

Table

Table 5 – Different treatments carbon balance by experiment, between days 10 and 17 PP, for the whole mass of leaves+adjacent stems in the 20 cm below the bract zone.

Carbon balance, whole mass of leaves and adjacent stems, in an average plant						
	Postproduction treatment	$\Delta Total_{L+S}$*	TLS**	Total consumption by TLS*	Total import*	Daily import ***
2002 Experiment	WATER	-50.703	0.213	35.855	-14.849	-2.121
	STS	-45.199	0.150	25.220	-19.979	-2.854
	NAA	-54.856	0.218	36.631	-18.225	-2.603
	STS+NAA	-65.279	0.280	47.114	-18.165	-2.595
2003 Experiment	WATER	-22.996	0.260	43.727	20.731	2.962
	STS	-8.933	0.330	55.500	46.567	6.652
	NAA	-24.288	0.351	59.003	34.715	4.959
	STS+NAA	-17.553	0.496	83.341	65.788	9.398

$\Delta Total_{L+S}$ =Variation in the leaf+adjacent stems carbohydrate levels.
TLS= leaf+adjacent stems respiration rate for the 20 cm below bract zone.
*(mg glucose.average plant^{-1});
**(mg glucose.average plant^{-1}. h^{-1});
***(mg glucose.average plant^{-1}.day^{-1}).

Figure

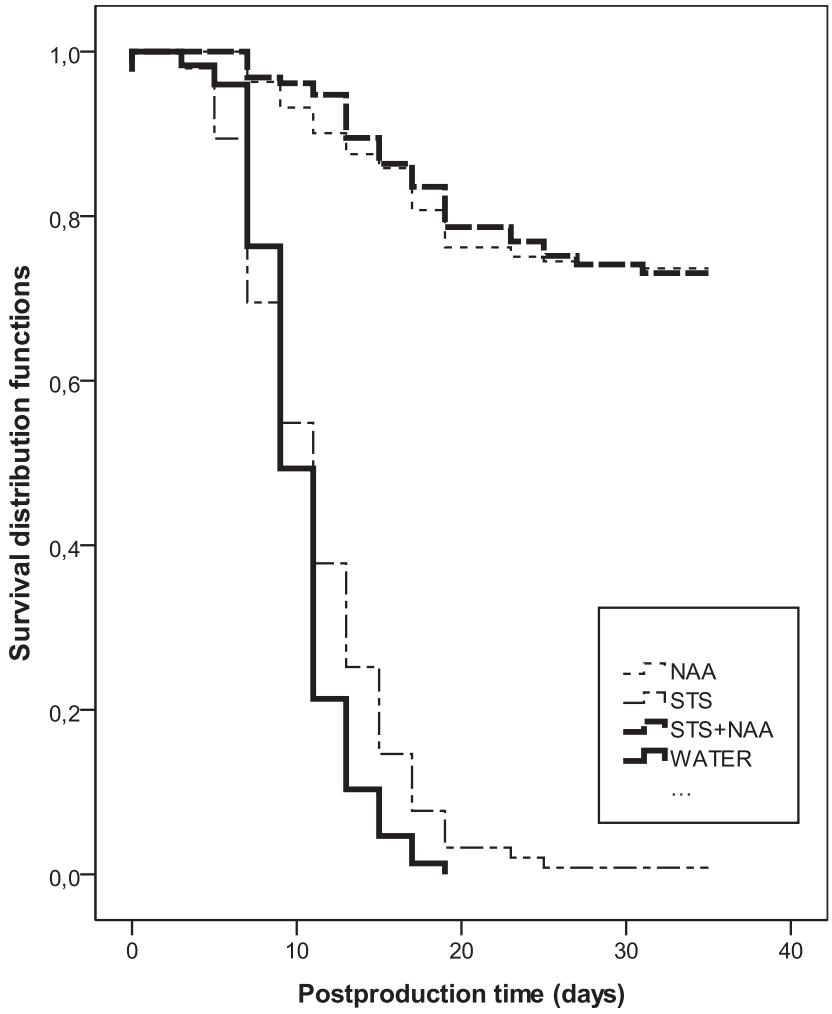

Fig. 1 – Kaplan-Meier estimates survival functions describing probability that a bract survive to time (t), in plants sprayed with WATER, STS, NAA and STS+NAA.

Figure

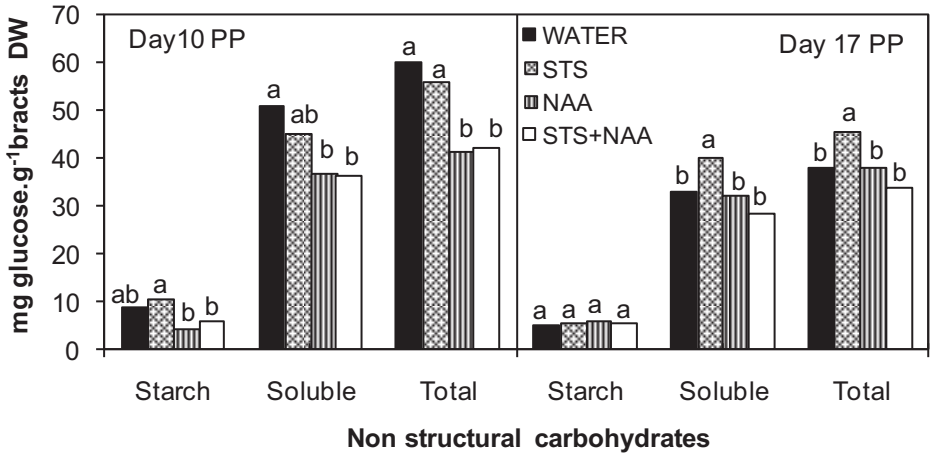

Fig. 2- Bracts starch, soluble and total non-structural carbohydrates for the different treatments (WATER, STS, NAA and STS+NAA) and the two postproduction days (days 10 and 17 PP). Bars are the means for the two experiments and, bars with different letters, within each day PP and carbohydrate type, are significantly different for Duncan's New Multiple Range Test, at P=0.05.

Figure

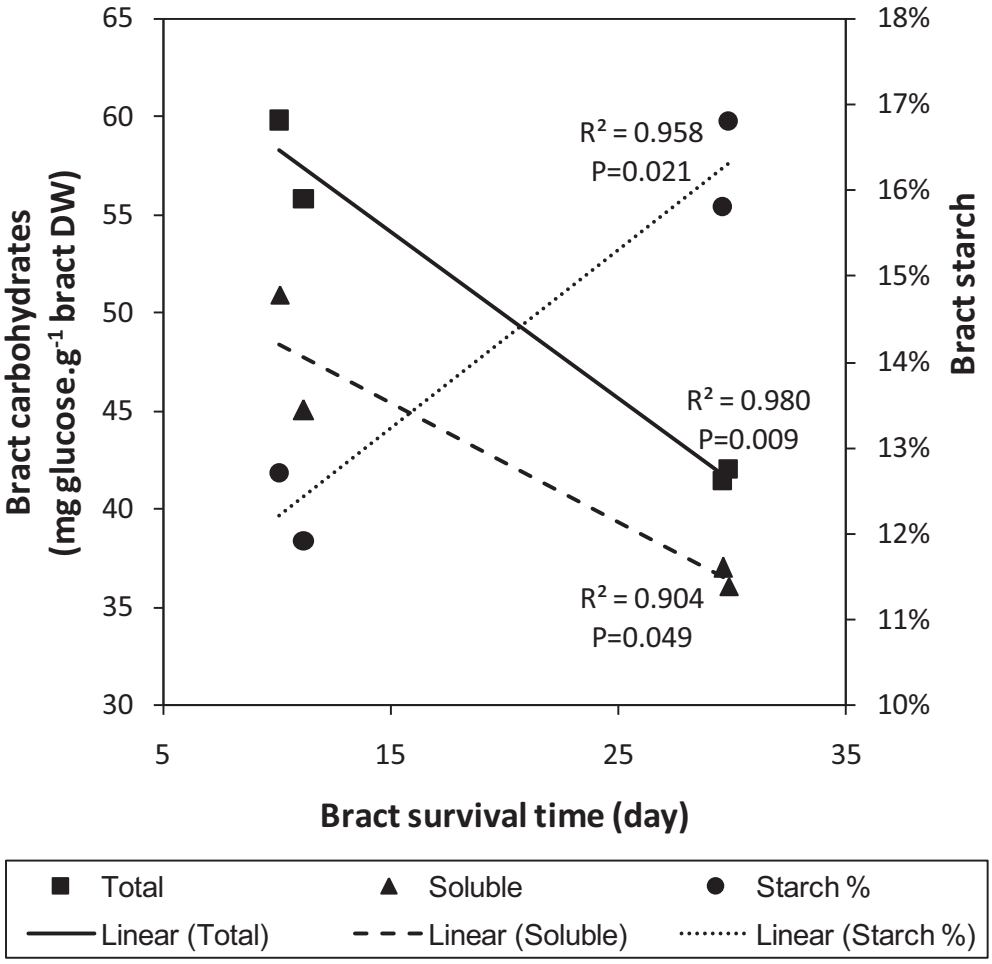

Fig. 3 - Linear regressions between bract survival time and bract non structural carbohydrate levels (total and soluble, measured at day 10 PP), and between bract survival time and bract starch percentage (measured at day 17 PP).

Figure

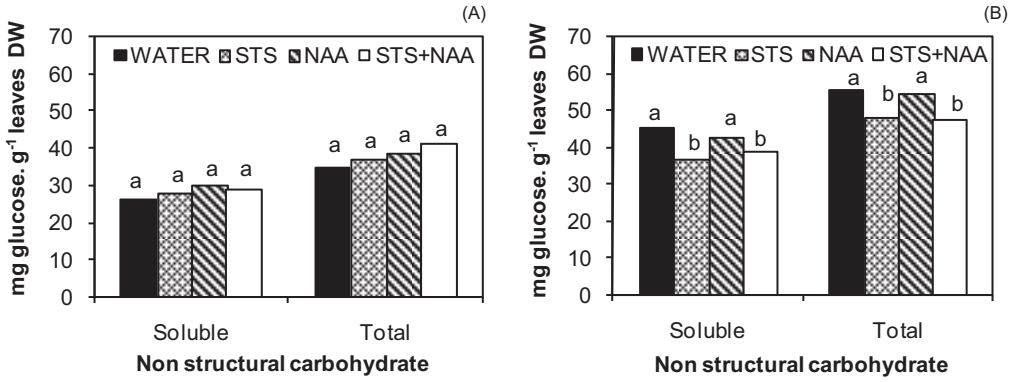

Fig. 4 – Leaf non structural carbohydrates: soluble and total for the different treatments (WATER, STS, NAA and STS+NAA). Experiment of 2002 **(A)** and 2003 **(B)**: Bars are means of two postproduction days (days 10 and 17 PP) and bars with different letters, within each carbohydrate type, are significantly different for Duncan's New Multiple Range Test, at *P*=0.05.

Figure

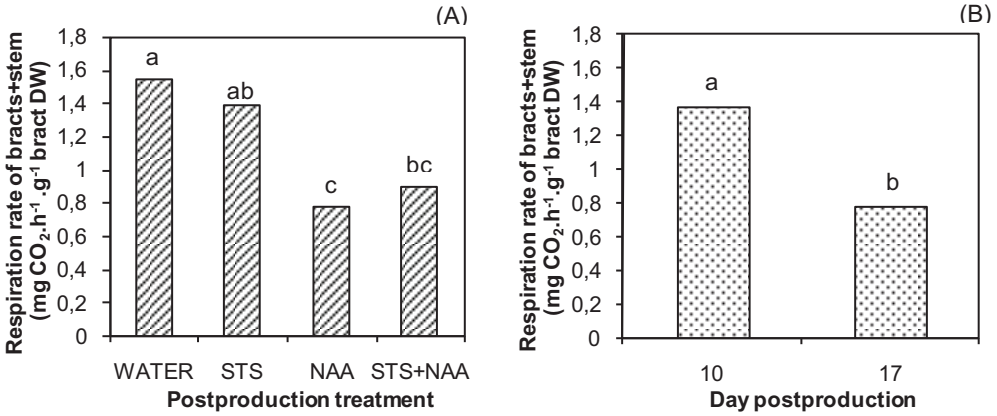

Fig. 5- Respiration rate of bract+stem (BS): **(A)** for the different postproduction treatments (WATER, STS, NAA and STS+NAA). Bars are means of two postproduction days (days 10 and 17 PP) and two experiments (2002 and 2003); **(B)** for postproduction days 10 and 17. Bars are means of four postproduction treatments (WATER, STS, NAA and STS+NAA) and two experiments (2002 and 2003). Bars with the same letter, are not significantly different for Duncan's New Multiple Range Test, at P=0.05.

Figure

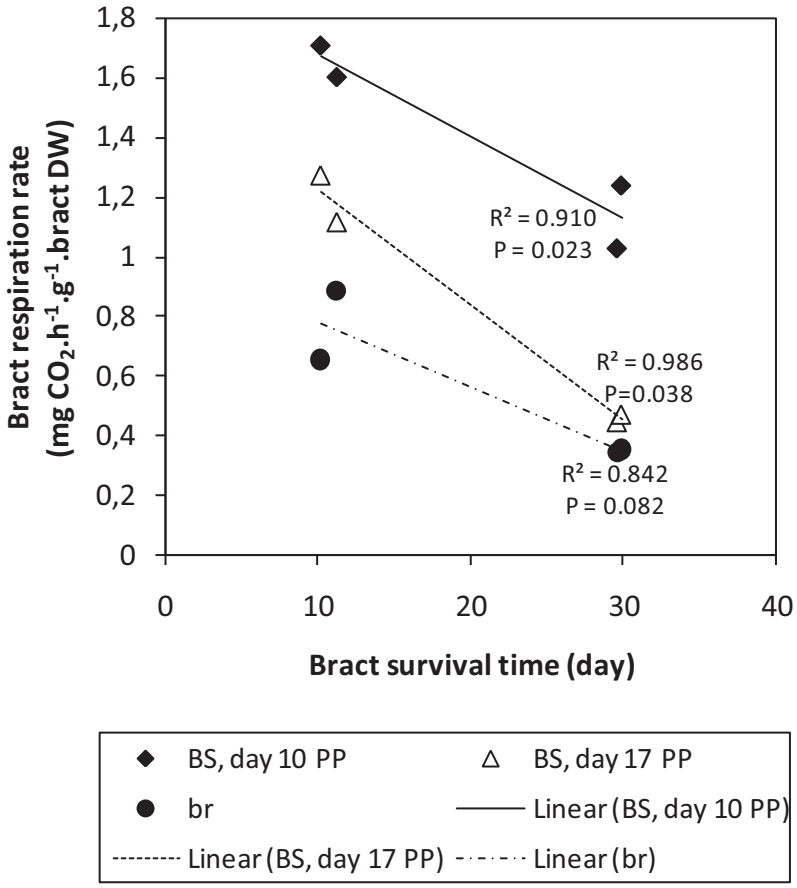

Fig. 6 - Linear regressions between bract survival time and bract respiration rate (measured together with the adjacent stems (BS) on days 10 and 17 PP, or estimated (**br**)).