

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

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12

13 **Abstract**

14

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

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

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

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

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

46

47 *Keywords:* Ornamentals; Postproduction; Postharvest; Auxin; Longevity; Keeping
48 quality.

49

50 **1. Introduction**

51

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

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

71 In the postproduction of flowering potted plants the main stress is low irradiance,
72 either acting through hormone mediated responses or, directly, through negative net
73 photosynthesis. Also, it is known that considerable amounts of carbohydrates are
74 necessary for the development/maintenance of the reproductive organs (Ho and Nichols,
75 1977; van Meeteren *et al.*, 1995; Waithaka *et al.*, 2001). The levels existing in these
76 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 maximiliani* Schröd (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; Borochoy 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,

102 2004). Auxin direct effect on respiration is rarely mentioned. Sacalis and Nichols
103 (1980) showed that the effect of the auxin 2,4-D on the respiration rate of carnation
104 flower, depended on the concentration applied. Compared to water controls, CO₂
105 production was accelerated by uptake of 4, 20 and 100 mg of 2,4-D.l⁻¹. However, 500
106 mg 2,4-D.l⁻¹ suppressed CO₂ and ethylene evolution and retarded senescence. In small
107 fruits, some studies involving auxin application (15, 25 or 50 mg NAA.l⁻¹), have shown
108 a reduction in dark respiration in the tissues of developing apples (Stopar *et al.*, 2001)
109 and medlar (Amorós *et al.*, 2004). In the whole plant level, depending on the dose and
110 time of application, auxins can either induce abscission or counteract it in citrus fruits
111 (Greenberg *et al.*, 2006; Gupta and Kaur, 2007; Yuan and Carbaugh, 2007).

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

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

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

131

132 **2. Materials and methods**

133

134 **2.1. General procedures**

135

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

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

149 At end of production, plants had approximately 60 cm height, at least ten bracts
150 completely developed and, at least one of them with an open flower (at anthesis). The
151 term bract, unless mentioned otherwise, refers to the bracts + flowers, i.e. an
152 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±1°C, no light).

164 At day 3 postproduction (PP) plants were unboxed, removed from the sleeves and
165 placed under interior conditions [21±1°C 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 CO₂-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 CO₂ 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 CO₂ 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 80°C. 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

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

206

207 **2.4. Calculations**

208 **2.4.1. Bract respiration**

209

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

$$213 \text{ TBS} = \mathbf{a} + \text{Bdw} \times \mathbf{br} + \text{Sdw} \times \mathbf{sr} + \mathbf{t} \times \text{DPP}$$

214 TBS – total respiration in bracts + adjacent stems (mg CO₂.h⁻¹)

215 **a** - constant

216 Bdw – bract dry weight (g)

217 **br** – bract respiration (mg CO₂.g⁻¹ bract dry weight.h⁻¹)

218 Sdw – stem dry weight (g)

219 **sr** – stem respiration (mg CO₂.g⁻¹ stem dry weight.h⁻¹)

220 **t** – change in respiration rate per day (mg CO₂.day⁻¹.h⁻¹)

221 DPP – day postproduction for the measurement

222

223 **2.4.2. Carbon balance**

224

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

228 $\mu\text{mol}\cdot\text{m}^{-2}\cdot\text{s}^{-1}$) 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 \times day PP \times 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⁻¹DW) was higher than at
302 day 17 PP (9 mg glucose.g⁻¹DW). The reverse happened with the soluble carbohydrates

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

312

313 **3.3. Respiration**

314 **3.3.1. Bracts**

315

316 Bract respiration rate (BS) was significantly affected by treatment and day PP (at
317 $P=0.0074$ and $P=0.0011$, respectively). Plants sprayed with WATER presented the
318 highest bract respiration rate, followed by intermediate values on plants treated with
319 STS and STS+NAA and, the lowest respiration rates occurred on bracts sprayed with
320 NAA (Fig. 5 A).

321 Respiration rate decreased from day 10 to day 17 PP (Fig. 5 B) by approximately
322 50% (on average of all treatments).

323

324 *Separation of bract from stem respiration*

325 At all postproduction treatments TBS was reasonably explained by bract and stem
326 dry weights and by postproduction day (Table 2). Estimated bract respiration rate (**br**)
327 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.

377 In the 2003 experiment, at day 17 PP, a higher LS, was related to a lower level of
378 leaf total carbohydrates, on that day [$LS = 2.197 - 0.0309 \times \text{total carbohydrates (mg}$
379 $\text{glucose.g}^{-1} \text{ leaf DW)}$; $R^2=0.893$ e $P=0.0552$]. However, it was not possible to establish
380 this correlation for 2002.

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

388 These results suggest that the different treatments did not influence substantially
389 the carbon balance in the leaves, and may suggest that the plants in the two experiments
390 had different leaf age. Unfortunately, photosynthetic rates were not measured and it is
391 unknown if it had any role in the balance. Percent of dry weight of leaves in the total
392 weight of leaves and adjacent stems differed with experiment: 52% in 2002 and 30% in
393 2003.

394

395

396 **4. Discussion**

397

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

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

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

422 Bracts have intermediate characteristics between leaves and petals and little
423 research has been done on these plant organs. In this study, when referring to bracts,
424 flowers are also included, and it is unknown in bougainvillea, despite their abscission as
425 a whole, to what extent these two organs behave in a similar way. As far as
426 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.

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

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

460 This study is consistent with previous works in which respiration rate is
461 negatively correlated with the longevity of the floral organs (Monteiro, 1991; Monteiro,
462 1993; Grossi *et al.*, 2003). In the previous studies, the causes of variation that
463 influenced the respiratory rates were often the genetic differences (different cultivars),
464 treatments that directly affect the speed of chemical reactions (such as temperature), or
465 substances such as STS that prevent ethylene action. Here, for the first time, it is shown
466 that the effect of NAA, in the maintenance of bracts of plants kept at low irradiance, is
467 accompanied by a decrease in the respiratory rate per gram of bract. This type of
468 response was previously found in apple (Stopar *et al.*, 2001) and medlar growing fruits
469 (Amorós *et al.*, 2004).

470 The meaning of the positive correlation between bract respiration rate and
471 carbohydrate level in the bracts is not so clear. We expected carbohydrate levels to be
472 lower in the treatments where their consumption was higher and the opposite happened.
473 It is possible that, if carbohydrate availability was a limiting factor, higher amounts of
474 available carbohydrates in the bracts allowed for higher respiration rates. However, it
475 does not make much sense that increased carbohydrate availability (although inducing
476 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

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

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

512

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648

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 ** \times 24 h \times 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 2 – Linear model $TBR = a + B_{dw} \times br + S_{dw} \times sr + t \times DPP$, 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 CO₂.h⁻¹.g⁻¹ bract DW, *² mg CO₂.h⁻¹.g⁻¹ stem DW, *³ mg CO₂.day⁻¹.h⁻¹

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			Total	Total	Daily
treatment	Δtotal_B^*	br **	consumption	import*	import***
			by br *		
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

ΔTotal_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 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			Total	Total	Daily
treatments	$\Delta\text{Total}_{\text{B+S}}^*$	TBS**	consumption	import*	import***
			by TBS*		
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

$\Delta\text{Total}_{\text{B+S}}$ = 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 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			Total	Total	Daily
	treatment	$\Delta\text{Total}_{L+S}^*$	TLS**	consumption by TLS*	import*	import ***
2002	WATER	-50.703	0.213	35.855	-14.849	-2.121
Experiment	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	WATER	-22.996	0.260	43.727	20.731	2.962
Experiment	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

ΔTotal_{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).

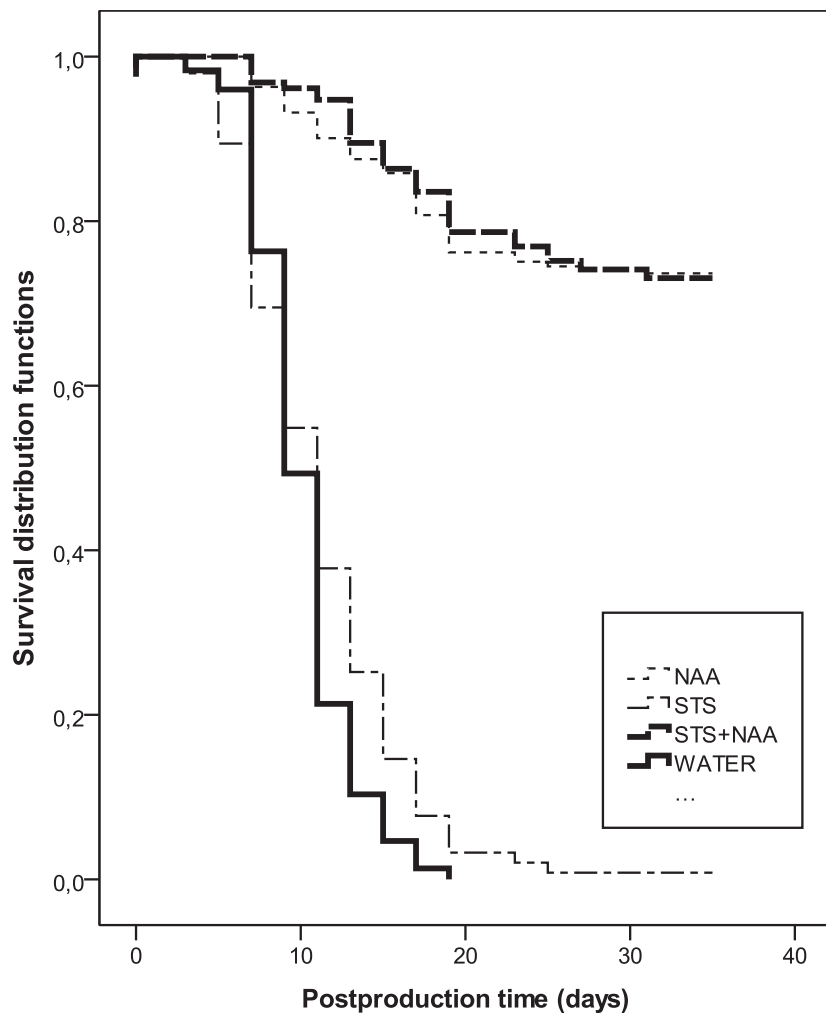


Fig. 1 – Kaplan-Meier estimates survival functions describing probability that a bract survive to time (t), in plants sprayed with WATER, STS, NAA and STS+NAA.

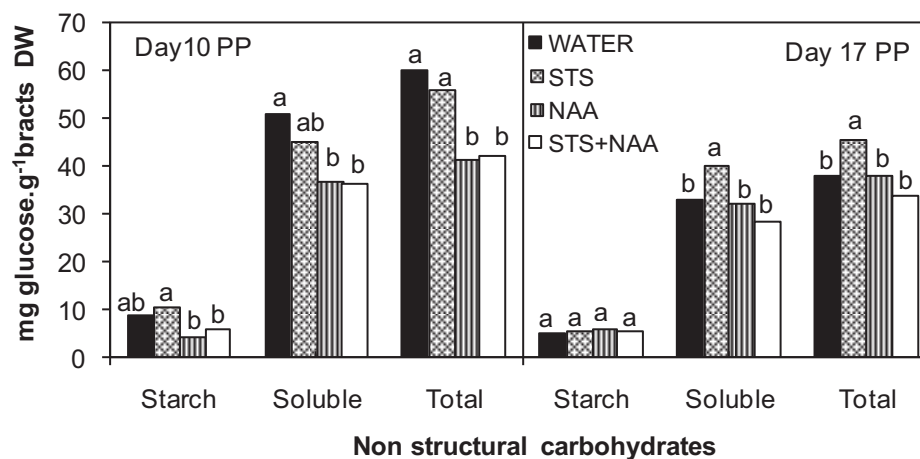


Fig. 2- Bracts starch, soluble and total non-structural carbohydrates for the different treatments (WATER, STS, NAA and STS+NAA) and the two postproduction days (days 10 and 17 PP). Bars are the means for the two experiments and, bars with different letters, within each day PP and carbohydrate type,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

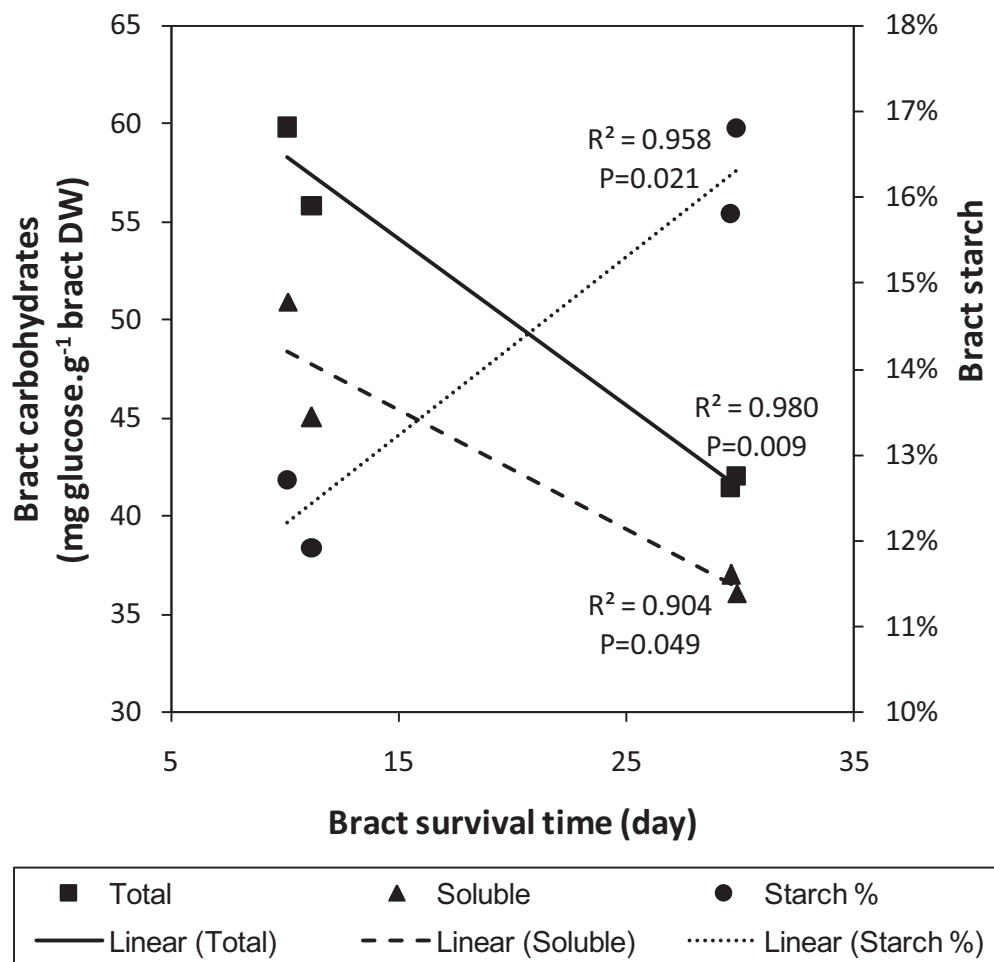


Fig. 3 - Linear regressions between bract survival time and bract non structural carbohydrate levels (total and soluble, measured at day 10 PP), and between bract survival time and bract starch percentage (measured at day 17 PP).

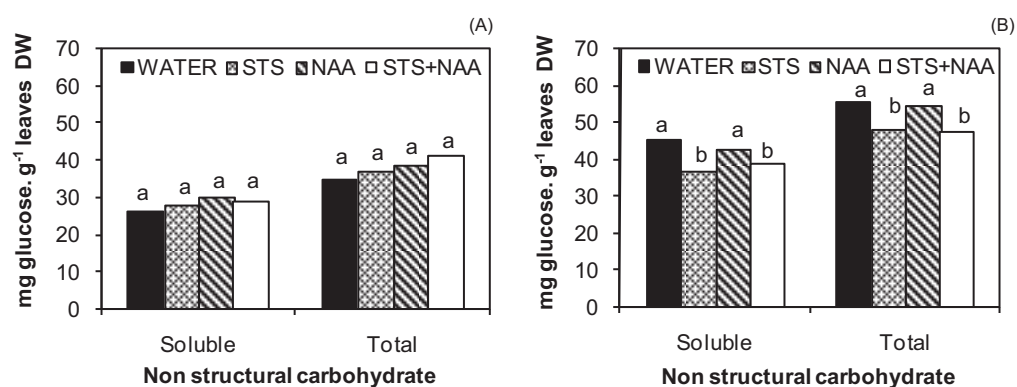


Fig. 4 – Leaf non structural carbohydrates: soluble and total for the different treatments (WATER, STS, NAA and STS+NAA). Experiment of 2002 (A) and 2003 (B): Bars are means of two postproduction days (days 10 and 17 PP) and bars with different letters, within each carbohydrate type, are significantly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

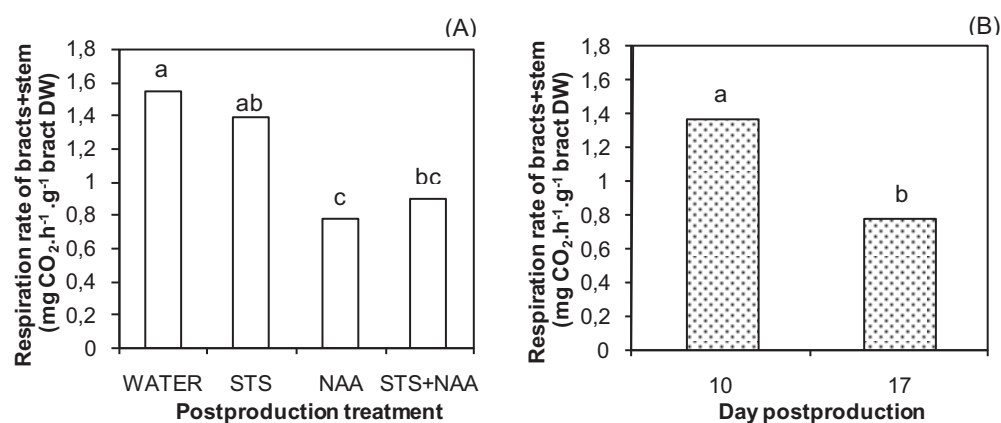


Fig. 5- Respiration rate of bract+stem (BS): **(A)** for the different postproduction treatments (WATER, STS, NAA and STS+NAA). Bars are means of two postproduction days (days 10 and 17 PP) and two experiments (2002 and 2003); **(B)** for postproduction days 10 and 17. Bars are means of four postproduction 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 $P=0.05$.

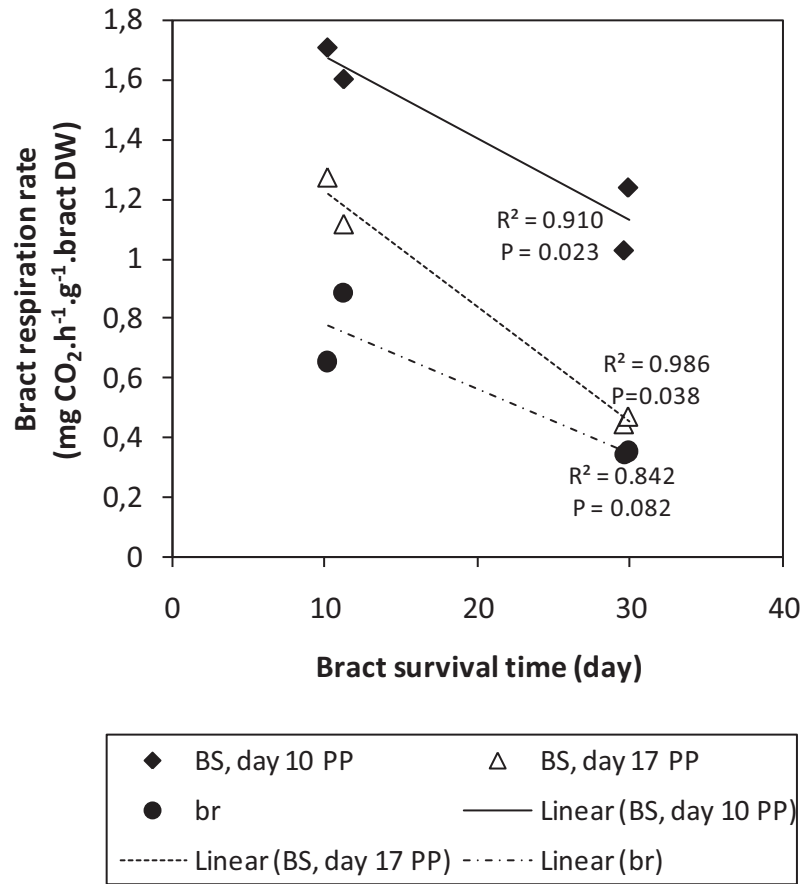


Fig. 6 - Linear regressions between bract survival time and bract respiration rate (measured together with the adjacent stems (BS) on days 10 and 17 PP, or estimated (br)).