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Do differences in plasticity during early growth lead to differing success in competition?

A test using four co-occurring annual *Papaver*

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Running head: Plasticity and competitive response

The authors have no commercial interest in the findings presented.

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Abstract

Plant species differ in their ability to transform available resources to biomass and to respond in a plastic way to environmental circumstances; we hypothesized that such differences among four weed taxa of *Papaver* would explain differences in their competitive response. We first compared two populations each of *Papaver rhoeas* L., *P. dubium* L. ssp. *dubium*, *P. dubium* L. ssp. *lecoqii* (Lamotte) Syme and *P. argemone* L., grown in greenhouse for six weeks in a nutrient gradient combined with two light treatments to elucidate possible differences in responses. As there were clear differences, a second experiment evaluated whether these differences also meant differences in competitive response, during early growth, when tested against two crops (wheat, rape). The assumption that competitive response was linked to the ability to transform nutrient and light to biomass was not supported: even though differences in extent of plasticity existed, the effect of competition was similar for the taxa. Thus, higher plasticity and ability to transform available resources to biomass did not lead to stronger competitiveness for *Papaver* during early growth.

Keywords: crop, nutrient, phenotypic plasticity, poppy.

Introduction

Closely related species as well as those with similar ecological affinity can differ substantially in the amount of biomass they produce when tested over a range of controlled environments (e.g. Milberg et al. 1999, Gianoli & Gonzales-Teuber 2005, Griffith & Sultan 2005, Muth & Pigliucci 2006, Barisic et al. 2006). Despite the potentially large importance for explaining success in competition in general (Daehler 2003, Cahill et al. 2005, Miner et al. 2005, Peacor et al. 2006, Richards et al. 2006), or in an arable land scenario (Håkansson 2003), there seems to be a paucity of direct experiments testing the assumption that a more plastic species is likely to compete better over a wide range of conditions than the less plastic one (Peacor et al. 2006, Richards et al. 2006). One exception is the study by Poorter and Lambers (1986) who showed that a more plastic genotype of *Plantago major* competed better than a less plastic one. Regarding invasive species, an invasive population of *Ceratophyllum demersum* was found to be more plastic than a non-invasive one (Hyldegaard & Brix 2012), five invasive species were generally more plastic than five native species on Hawaii (Funk 2008), but there was no general difference in extent of plasticity between exotic invasive species and native species when 40 species in Spain were pairwise compared (Godoy et al. 2011). However, a meta-analysis showed invasive species being generally more plastic than none-invasive species (Davidson et al. 2011).

In the present study, we focus on two aspects relevant for an arable field scenario: (1) What is the extent of variation regarding plasticity in ability to transform resources into biomass among closely related annual weeds? (2) Do such (possible) differences between species have any bearing on explaining differences in competitive response (competitive tolerance)? We addressed these questions in two greenhouse experiments involving four closely related taxa within the genus *Papaver* (Papaveraceae). The four taxa co-occur on

arable land in Sweden, but differ in their seriousness as weeds, making them a suitable group for investigation of possible underlying reasons for differences in performance in competition with other species. The first experiment aimed at describing the biomass produced under a range of environments as a way to evaluate the taxa's extent of plasticity in ability to transform resources into biomass, while the second experiment evaluated and compared their competitive response when grown with any of two crop species, as well as their competitive effect on the crops.

Materials and methods

Plant material

The selected taxa (Table 1) were four closely related *Papaver*, being rosette-forming facultative winter annuals. The seeds have a relatively strong dormancy, and the general dormancy and germination pattern explains how germination can occur mainly in autumns and springs in warmer and colder environments, respectively (Karlsson and Milberg 2007). The taxa have similar seed mass (Table 1) but differ in final height, with the flower stalk being longest for *P. rhoeas* and shortest for *P. argemone* (Jonsell et al. 2001). All occur on arable land in Europe, north to ca 60° in Sweden. The taxa differ in distribution by *P. dubium* spp *lecoqii* being restricted to the east of Sweden (Jonsell et al. 2001) and, in contrast to *P. rhoeas* and the two *P. dubium*, *P. argemone* is not present in southernmost Europe or in Northern Africa (Hultén and Fries 1986, Kadereit 1988). *Papaver rhoeas* occurs in addition as a weed worldwide (Holm et al. 1997). In Scandinavia, all four taxa co-occur in various constellations and we have observed all four in the same field (personal observation). *Papaver rhoeas* is a close relative of the two *P. dubium* subspecies, while *P. argemone* is more distantly related (Carolan et al. 2006). As annual weeds in general, the four taxa exhibit substantial phenotypic plasticity (McNaughton and Harper 1964).

For each taxa, we used two seed batches (replicates) originating from each of two wild weed populations southern Sweden (Table 1). For each batch, seeds had been collected from ca. 30 plants. The seeds in a batch were thoroughly mixed, dried indoors about ten days at ca 20°C and then stored in a freezer (-12°C) until used.

Common greenhouse procedures

Experiments were conducted in a greenhouse, where seedlings were grown under a range of conditions in narrow plastic pots placed in special trays designed to hold 98 pots (Ray Leach “Cone-tainer” Single Cell System, USA). Pots had a volume of 164 mL, a height of 210 mm and drainage holes in the bottom. Washed quarts sand (Baskarpsand 35, AB Baskarpsand, Habo, Sweden) was used as growth medium. The sand had been screened through 0.125 and 0.71 mm mesh and after screening 80% of the sand had a grain-size between 0.18 and 0.50 mm. The content of silica was 91.3%.

The greenhouse was temperature-regulated, with target temperatures set to 20°C in daytime and 10°C in night (12h/12h). The temperature was monitored during the experiments (Tinytag, Gemini Data Loggers). Incoming daylight was supplemented by lamps (Osram Vialox 400 W Nav-T Super (Son-T Plus)). The trays were placed on a table; which in turn was placed centrally in the greenhouse. The plants were watered with tepid tap-water every to every third day, depending on their size and weather.

Nutrient gradients were created by adding different amounts of small granules of a slow-release fertilizer (Osmocote: Start 2-3 month. Grace-Sierra, International, Heerlen, the Netherlands) that had been sieved to reduce their variation in size, resulting in ca. 2 mm diameter. This fertilizer consists of 16% N, 3.5% P, 9.1% K, 1.2% Mg and trace elements.

First experiment: intra-clade differentiation in ability to turn resources into biomass

Seeds were sown, in January 2003, on two sheets of filter paper (90 mm, Munktell 1003) in Petri dishes. The filter papers were moistened with gibberellic acid (1000 mg L⁻¹ of GA₃, Sigma Chemical Co., USA) to enforce germination. The Petri dishes were sealed with parafilm and incubated in light/darkness (12h/12h) and in different temperature regimes, *P. dubium* ssp. *lecoqii* in 25/15°C, *P. dubium* ssp. *dubium* in 20/10°C, *P. argemone* and *P. rhoeas* in a constant temperature of 5°C. These temperatures regimes were selected based on germination experiments on these seed batches (Karlsson & Milberg 2003, 2007). Two of the collections (*P. dubium* ssp. *dubium* from Tallbacken and *P. dubium* ssp. *lecoqii* from Vadstena) were particularly difficult to germinate and therefore, some Petri dishes were also placed at other temperature regimes (5, 15/5, 20/10, 25/15°C). When a seed had germinated to the extent that the radicle was visible, about 1 mm, the germinant was transplanted to the plastic pots in the greenhouse. Initially, there were three seedlings per pot and the trays were covered with transparent plastic for 2-6 days to enhance seedling establishment. Two to three weeks after planting, the pots were thinned so that only one plant remained in each pot.

Before transplant, the pots had been filled with sand to about 25 mm from the rim. Then, the nutrient granules were added and finally, the pots were topped up with 15 mm of additional sand. There were 9 nutrient treatments (0, 1, 2, 4, 8, 16, 32, 64, 128 granules) combined with two light treatments (full light and shaded) in a full factorial design with seven replicates. In total, there were 16 trays with 63 pots in each. To make the environment as similar as possible for all plants, the trays were rearranged on the table every second day.

The light at noon in the full light treatment was measured with a photometer at nine measuring points at germinant level. On a cloudy day, 218 $\mu\text{mol m}^{-2} \text{s}^{-1}$ was recorded and on a sun hazy day 282 $\mu\text{mol m}^{-2} \text{s}^{-1}$. In the shading treatment, the trays were placed in boxes, one tray per box, made from particle board and with four layers of grey plastic mosquito net (mask width 1 mm, Poly-Produkter, Göteborg, Sweden) on the top. There was a 200 mm

distance between the surface of the pots and the net. This shading treatment reduced light to 20% of that of the full light (as recorded at noon), a reduction typical of a relatively dense crop stand in Sweden (Andersson & Milberg 1996), and which gives a difference in light intensity that affected 46 grassland species studied by Semchenko et al. (2012). Average daily maximum temperature during the experiment was 25.8°C (SD 4.7) while average daily minimum temperature was 9.5°C (SD 0.7).

The harvest started on the 25th of March and continued to the 16th of April. By harvest, each plant had spent 44 days in the greenhouse. The plants were gently removed from their pots and the roots were carefully washed in water. The maximum length of roots (defined as root plus hypocotyl) was measured stretched out on a sheet of millimetre graded paper, as was shoot length (i.e. epicotyl) in case of etiolation (only recordable in the shaded treatment). Biomass of shoots and roots were noted after being dried in 75°C for a minimum of 24 h.

Second experiment: intra-clade differentiation in competitive response

In January 2004, *Papaver* seeds were exposed to gibberellic acid as above. This time, the Petri dishes with filter paper were placed in a greenhouse at approximately 25/15, except for *P. argemone* that was placed at 20/10. One seed population of *P. dubium* spp. *dubium* germinated poorly, so some seeds were also subjected to a higher gibberellic acid solution (2000 mg L⁻¹).

Autumn-sown cultivars of two crop species were used as competitor: winter wheat *Triticum aestivum* L. ‘Olivin’ and winter rape *Brassica napus* L. ‘Silvia’. Seeds were germinated in Petri dishes (without GA₃) in the greenhouse. As the rape seeds had been chemically treated against insects, the testa was removed before the germinant was transplanted to pots, as a precaution.

Combinations of two germinants, one crop and one *Papaver*, was simultaneously planted in the narrow pots containing different amounts of nutrients. In this experiment, the nutrient gradient consisted of 0, 1, 4, 16 and 64 granules. There were five replicates per treatment. In addition, there was a series of control plots containing single specimens of the eight *Papaver* populations as well as single specimens of the two crops. In total, there were 650 pots, randomly placed in trays.

Light, measured at germinant level, was 254 and 372 $\mu\text{mol m}^{-2} \text{s}^{-1}$ on a cloudy and sunny day, respectively. Average daily maximum temperature during the experiment was 21.5°C (SD 3.08) while average daily minimum temperature was 10.6°C (1.64). The experiment was terminated after six weeks growth in the greenhouse when biomass of crop and weed was recorded. Observations and measurements in the first experiment had shown that the four taxa differed in biomass accumulation, but were otherwise morphologically very similar when grown in full light. This was not unexpected, considering how closely related they are, and a justification for focusing on biomass as the main outcome variable in the competition experiment. As the roots of the paired plants were, in many cases, very difficult to separate, only above-ground biomass was considered.

Statistical analyses

First experiment

The four taxa have similar seed mass (Table 1), and are comparatively similar in seedling morphology, which simplifies comparison of the biomass produced. The minimum size of the plants grown (without nutrients and in reduced light) would be mainly determined by seed reserves, that are similar (and small) in these four taxa. The maximum plant size, however, would be mainly determined by possible intrinsic properties of growth in a particular species. Therefore, we analysed this experiment with ANOVA.

Of the 1008 pots with plants, 955 contained living plants at harvest. The 53 losses were not evenly distributed among the treatments; most losses were found at the highest nutrient level ($N = 23$), and within two populations (Tallbacken $N=19$; Omberg $N=14$) and one species (*P. dubium* spp. *dubium* $N=21$). As we used population averages in the statistical analyses, this unbalanced occurrence of missing values had no practical consequences.

We conducted two ANOVAs, with (i) average $\log_{10}$ -transformed biomass, and (ii) average root-mass/shoot-mass as response variables, using the following factors: taxon, light/shade, nutrient and their interaction factors. Of interest to our aims were “taxon” and the interaction factors that involved “taxon”.

In the early part of life, the species studied are very similar in morphology, and only one of the other variables recorded turned out to vary between species: the ability to etiolate in shade. As these differences were small, and on an integer scale, we used GLM (poisson distribution, log-link) to evaluate differences between species. Finally, for display purposes, we returned to the raw data ($N=955$) and fitted species-wise lowess (locally weighted scatterplot smoothing) curves (stiffness 0.5) per species along the nutrient gradient.

Second experiment

Of the 400 pots, 38 were lost due to mortality of *Papaver* or the crop. These missing values were evenly distributed among the treatments. To be able to pair data on plants grown with and without competition, we used population average per treatment.

The effect of competition has been evaluated in numerous ways, mainly through indices (Weigelt & Jolliffe 2003). We followed the protocol suggested by Lamb et al. (2006) which aim at finding the simplest model possible for accurate description of data. In this stepwise procedure, we first assumed that size-dependence might exist, and fitted the model (1) below to the global data:

$$\text{Biomass}_{\text{mix}} = k_1 + k_2 * (\text{Biomass}_{\text{control}})^{k_3} \quad (1)$$

where $\text{Biomass}_{\text{mix}}$ is the biomass of the target taxon when grown in mixture and $\text{Biomass}_{\text{control}}$ when it is grown without competition; k_1 , k_2 and k_3 are constants. Second, eliminating k_1 did not improve the model (AIC increased from 299.1 to 299.8), suggesting that size-dependence can be ignored. Third, setting $k_3=1$ only slightly improved the explanatory power of the model (AIC decreased from 299.8 to 298.7), suggesting that a linear model would not be much inferior to a more complex one. Hence, we turned to ANOVA for analyses, using $\text{Biomass}_{\text{control}}$ as covariable and “nutrient” (N=5) and “weed species identity” (N=4) as categorical variables (following Jasiński & Bazzaz 1999, Cahill et al. 2005), and using the two populations per species as replicates. To reduce the risk for a Type I error, we conducted one analysis per crop and one with both crops together, i.e. three ANOVAs in total.

For display purposes, we used residuals from species-wise ANOVAs using nutrient level as the only explanatory variable. Thereby, we had eliminated the effect of nutrients and could express the results, per *Papaver* taxa or crops, as deviations from the average. In this way we could highlight possible effects of competitors and differences between species.

Results

First experiment

Biomass: There were highly significant differences between taxa, but the interaction factors involving “taxon” were non-significant (Table 2). As expected, light conditions and nutrient availability greatly influenced biomass (Table 2). There was also a strong interaction between light and nutrient (Table 2), probably reflecting a slower growth in the shade, preventing plants to take full advantage of the available nutrients (Fig. 1). It seems that the nutrient gradient in the experiment encompassed the optimum, as all the measured characters, with one exception (above ground biomass in light treatment), plateaued or decreased for all taxa

at the highest nutrient level (Fig. 1). On average, *P. rhoeas* produced most biomass (significantly larger than all other taxa, in a Tukey HSD), while *P. dubium* spp. *dubium* produced least. Of the two intermediate taxa, *P. dubium* spp. *lecoqii* produced slightly more biomass than *P. argemone*, but not significantly so (Tukey HSD).

Root/shoot ratio: The ANOVA of root/shoot ratio (Table 2) revealed similar pattern as the one for biomass. i.e. taxa differed in their root/shoot ratios (Fig. 2).

Etiolation: No shoot elongation was recorded in light, but species differed in their elongation in shade (Wald $\chi^2_{(3)}=237.4$; $P<0.0001$). *Papaver argemone* elongated least, *Papaver dubium* spp. *dubium* and *P. dubium* spp. *lecoqii* were intermediate and quite similar in their response while *P. rhoeas* was the taxon that elongated most (Fig. 1).

Second experiment

All *Papaver* were negatively affected by competition with crop (Fig. 3a), but none of the ANOVAs conducted detected an effect of weed species (i.e. taxa, Table 1) on the biomass of plants subjected to competition (both crops together $F_{(3,39)}= 1.386$, $P=0.261$; rape $F_{(3,19)}= 1.088$, $P=0.378$; wheat $F_{(3,19)}=1.580$, $P=0.227$; Fig. 3a).

As expected, considering the relative short-term nature of the experiment, the crops, that are large-seeded, were not much affected by the presence of a weed (Fig. 3b). A preliminary t-test (on log-transformed biomass data) indicated that the presence of a weed had a very small effects on the rape crop (average difference rape -0.0446, $t=-1.91$; $P=0.063$) and a negligible one on wheat (+0.0420, $t=1.38$, $P=0.176$). Hence, we did not consider data on the crops grown with or without competition further.

Discussion

Ability to transform resources into biomass

The four related *Papaver* taxa (phylogenetics revealed by Carolan et al. 2006) differed substantially in size and morphology after 44 days growth in a variety of growth conditions (Fig. 1). There was, however, no apparent phylogenetic pattern in growth capacity among the four species: the phylogenetically most distant taxon, *P. argemone* (Carolan et al. 2006), performed intermediately with the two sub-species of *P. dubium*, the two latter differing especially regarding above-ground biomass response to the gradient of nutrients (Figs. 1, 4). *Papaver rhoeas*, the taxon that responded strongest to the gradient (Fig. 1), belongs to the same clade as *P. dubium* but not the same as *P. argemone* (Carolan et al. 2006). Hence, differentiation in capacity to exploit resources seems to develop much faster than speciation (Fig. 4).

The root/shoot ratios were low in shaded conditions for all the taxa (Fig. 2). It is apparent that the plants are allocating more to growing green parts, to maximise their photosynthetic capacity, than to their roots. For the plants grown in full light conditions, the ratios between root and shoot were rather similar over the range of plant sizes involved (Fig. 2).

The response invoked by shade differed quantitatively among species, as judged by the etiolation recorded (Fig. 1): from a maximum of 3 to 9 mm. Even after accounting for differences in plant size, etiolation of *P. d. dubium* was twice that of *P. argemone*, taxa that produced similar amounts of biomass (Fig. 1). Hence, even related species, occurring within the same habitat, may differ in extent of plasticity (Figs. 1, 2; cf. Griffith & Sultan 2005) and in general allocation of biomass (Fig. 1; Jia et al. 2010).

Plasticity as predictor of competitiveness

In contrast to Poorter and Lambers' (1986) study of *Plantago major*, we were unable to show a difference in competitive response, or competitive effect, among the closely related *Papaver*

species (Fig. 3a) despite the fact that they differed in their ability to transform resources into biomass; seed mass is similar (Table 1) but biomass produced without nutrient differed between taxa (Fig. 1). Could our inability to document differentiation in competitive response, as well as competitive effect, be due to the relatively short duration of our experiment, i.e. that competition had not yet manifesting itself in biomass loss? This was, as expected, the case for the crop data (competitive effect, Fig. 3b), but the *Papaver* species were severely hampered by competition (Fig. 3a), leaving plenty of room for manifestation of inter-taxon differences in competitive response. Thus, the theory that higher extent of plasticity gives a stronger competitor was not supported for *Papaver* during early growth.

Analogous to competition, high extent of plasticity is also assumed to be correlated to invasiveness. This theory was supported for different populations of one aquatic species (Hyldegaard & Brix 2012) and by Funk (2008), when five invasive species were compared with five native. However, the theory was not supported when 20 native and 20 exotic invasive species were compared (Godoy et al. 2011). Funk (2008) and Goday et al. (2011) included, respectively, one and five pairs of species belonging to the same genus. Of these, there were two pairs in which the exotic species was more plastic than the native. Thus, as for competitiveness (Fig. 3), higher extent of plasticity is not necessarily an explanation to stronger invasiveness (Godoy et al. 2011), even though invasive species are generally more plastic than none-invasive species (Davidson et al. 2011).

Field implications

Transferring these results outside the greenhouse, one would expect that *P. rhoeas* is the one best fitted in a modern agricultural landscape. It had the highest biomass, even at low levels of nutrient, and it had the highest values of etiolation. Along the same arguments, *Papaver argemone* would be the least fitted. In fact, the former species is regarded a serious weed at

several localities (Holm et al. 1997) and seems to be increasing, albeit presumably because of development of herbicide resistance, while the latter is rare and probably decreasing (Aronsson 1999, Nilsson & Nilsson 2004). Performance during later stages of growth may determine the outcome for these weeds in competition with crops. Despite developing similarly during early growth when subjected to competition (Fig. 3), the four taxa differ in final height, with *P. argemone*, *P. dubium* and *P. rhoeas* reaching 66, 80 and 100 cm, respectively (Jonsell et al. 2001). Thus, *P. rhoeas* is larger than the other during early growth without competitor (Fig. 1) and higher when mature in the field (Jonsell et al. 2001). The ability to grow large may itself be the reason for this taxa being the most serious weed of the *Papaver* taxa studied here, despite the fact that differences could not be recorded during early growth when competition occurred.

In conclusion, even closely related species can differ substantially regarding plasticity in biomass allocation and nutrient utilization, but such differences must not necessarily lead to differences in competitive response during early growth. However, biomass allocation and nutrient utilization will probably affect final size and other characteristics of species, which can explain differences in competitive response at maturity, which in turn may be part of the explanation to differences in worldwide distribution also of other closely related species than the *Papaver* studied here. It remains for future studies of groups of closely related species to reveal the general importance of plasticity on competitive response.

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422 **Figure legends**

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Figure 1

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429 **Fig 1.** Attributes of four *Papaver* taxa, two populations of each, after six weeks of growth in
430 seven fertilization levels and two light conditions: full light and shaded (20 % of the intensity
431 in full light). Curves are fitted lowess (locally weighted scatterplot smoothing) to data on
432 individual plants. Root length was measured as the stretched longest root plus hypocotyl, and
433 etiolation as the length of epicotyl (present only in shadow).

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Figure 2

Fig. 2 Root/shoot ratio of four *Papaver* taxa, two populations of each, after six weeks of growth in two light conditions; full light and shade (20 % of the intensity in full light). Grey line indicate root/shoot ratio 1.

Figure 3

447 **Fig. 3** Boxplots of residuals from taxon-wise ANOVAs of four *Papaver* taxa, two
448 populations of each, grown using nutrient level and as the only explanatory variable. 3a)
449 Weed species (*Papaver*), and 3b) Crop species.

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455 **Fig. 4** Principal phylogeny (from Carolan et al. 2006) of four *Papaver* taxa (two populations
456 of each) studied regarding growth response to nutrients and light; extent of plasticity in ability
457 to exploit recourses during early growth found to be low, intermediate or high.

458

Table 1. Places and dates of collections, and seed characteristics, for *Papaver* taxa used to study biomass allocation and competitive response.

<u>Taxon</u>	<u>Place of collection</u>	<u>Date of collection</u>	<u>Seed mass (mg)</u>	<u>Embryo length (mm (SD; N=20))</u>
<u><i>P. argemone</i></u>	<u>Omberg (58°17'N 14°40'E)</u>	<u>15 July 2002</u>	<u>28</u>	<u>0.40 (0.046)</u>
<u><i>P. argemone</i></u>	<u>Ledberg (58°26'N 15°28'E)</u>	<u>15 July 2002</u>	<u>27</u>	<u>0.43 (0.059)</u>
<u><i>P. dubium</i> ssp. <i>dubium</i></u>	<u>Knivinge (58°29'N 15°29'E)</u>	<u>17 July 2002</u>	<u>21</u>	<u>0.38 (0.032)</u>
<u><i>P. dubium</i> ssp. <i>dubium</i></u>	<u>Tallbacken (58°25'N 15°29'E)</u>	<u>17 July 2002</u>	<u>25</u>	<u>0.41 (0.034)</u>
<u><i>P. dubium</i> ssp. <i>lecoqii</i></u>	<u>Glänås (58°20'N 14°50'E)</u>	<u>17 July 2002</u>	<u>21</u>	<u>0.29 (0.052)</u>
<u><i>P. dubium</i> ssp. <i>lecoqii</i></u>	<u>Vadstena (58°27'N 14°53'E)</u>	<u>25 Aug. 2002</u>	<u>24</u>	<u>0.28 (0.034)</u>
<u><i>P. rhoeas</i></u>	<u>Vadstena (58°27'N 14°52'E)</u>	<u>19 July 2002</u>	<u>26</u>	<u>0.51 (0.071)</u>
<u><i>P. rhoeas</i></u>	<u>Strå (58°24'N 14°54'E)</u>	<u>19 July 2002</u>	<u>23</u>	<u>0.40 (0.059)</u>

Table 2. ANOVA on data of four taxa of *Papaver* grown for 44 days in a greenhouse under different light and nutrient conditions.

	<u>DF</u>	<u>MS</u>	<u>F</u>	<u>P</u>
<u>Average total biomass</u>				
<u>A Taxon</u>	<u>3</u>	<u>0.469</u>	<u>27.5</u>	<u><0.000001</u>
<u>B Light condition</u>	<u>1</u>	<u>11.8</u>	<u>690</u>	<u><0.000001</u>
<u>C Nutrient</u>	<u>8</u>	<u>4.85</u>	<u>284</u>	<u><0.000001</u>
<u>A*B</u>	<u>3</u>	<u>0.0250</u>	<u>1.46</u>	<u>0.231</u>
<u>A*C</u>	<u>24</u>	<u>0.0131</u>	<u>0.769</u>	<u>0.761</u>
<u>B*C</u>	<u>8</u>	<u>0.458</u>	<u>26.9</u>	<u><0.000001</u>
<u>A*B*C</u>	<u>24</u>	<u>0.0139</u>	<u>0.816</u>	<u>0.705</u>
<u>Error</u>	<u>72</u>	<u>0.0170</u>		
<u>Root/shoot ratio</u>				
<u>A Taxon</u>	<u>3</u>	<u>0.178</u>	<u>8.80</u>	<u>0.000048</u>
<u>B Light condition</u>	<u>1</u>	<u>7.22</u>	<u>356</u>	<u><0.000001</u>
<u>C Nutrient</u>	<u>8</u>	<u>1.11</u>	<u>54.9</u>	<u><0.000001</u>
<u>A*B</u>	<u>3</u>	<u>0.0478</u>	<u>2.36</u>	<u>0.0787</u>
<u>A*C</u>	<u>24</u>	<u>0.0188</u>	<u>0.929</u>	<u>0.565</u>
<u>B*C</u>	<u>8</u>	<u>0.101</u>	<u>4.98</u>	<u>0.000062</u>
<u>A*B*C</u>	<u>24</u>	<u>0.0262</u>	<u>1.29</u>	<u>0.200</u>
<u>Error</u>	<u>72</u>	<u>0.0203</u>		