GROWTH AND PHOTOSYNTHETIC RESPONSE OF *SORGHUM BICOLOR* CULTIVARS PATO, P9405, P9406 AND MACIA TO NITROGEN AVAILABILITY AND INFECTION BY THE HEMIPARASITIC WEED *STRIGA HERMONTHICA*.

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Sokoine University of Agriculture, Tanzania

WORKING PAPER

GROWTH AND PHOTOSYNTHETIC RESPONSE OF *SORGHUM BICOLOR* CULTIVARS PATO, P9405, P9406 AND MACIA TO NITROGEN AVAILABILITY AND INFECTION BY THE HEMIPARASITIC WEED *STRIGA HERMONTHICA*.

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Cover photo (Simon Pierce). *Striga hermonthica*, a hemiparasitic witchweed infecting cereal crops in sub-Saharan Africa.

Preface

Striga species, the so-called witchweeds, are widespread on the fields of small holder farmers in semi-arid areas of Eastern and Southern Africa. These noxious parasitic weeds principally attack and reduce the yield of finger millet, maize, sorghum and upland rice in these regions. In many areas it is the crops of resource-poor households which are affected by these weeds. They impose an additional stress with which people, who have little capacity for investment in crop production, have to cope in an environment characterised by marginal rainfall for cropping and declining soil fertility. Since 1996 staff from the Department of Agricultural Research, and Sokoine University in Tanzania and, Natural Resources Institute and University of Sheffield in UK have been collaborating in studies aimed at developing integrated *Striga* management practices. Studies are being undertaken on-station and on infested farmers fields in affected communities in the Central, Eastern, Lake and Southern Highlands agricultural zones in Tanzania, with laboratory studies at the University of Sheffield. On-farm studies are implemented in collaboration with District Agricultural Extension. Current work emphasises:

- the farmer assessment of tolerant sorghum cultivars and cultural practices which reduce the impact of the parasite;
- the development of learning tools which can provide farmers with a greater understanding of the *Striga* problem;
- understanding the differential performance of sorghum cultivars under a range of levels of soil fertility;
- the identification of traits which confer tolerance to *Striga* in maize;
- farmer assessment of cultural practices which reduce the impact of *Sriga* in upland rice

The following reports summarising previous results are obtainable from:

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Striga distribution and management in Tanzania – Proceedings of a stakeholder workshop. (1999) Riches, C.R. (Ed.)

Integrated *Striga* control in cereals for small scale farmers in Tanzania: Project Technical Report (2000) Mbwaga A.M.

Striga research activities in Dodoma region: Evaluation of research trials 1999/00 season (2000) Lamboll (Ed.)

Striga research activities in Central Zone and Lake zone of Tanzania: Evaluation of on-farm research trials 2000/01 season (2001) Lamboll R, Hella J, Mbwaga A & Riches C.

Striga research activities in Central, Eastern and Southern Highlands zones of Tanzania: On-station and on-farm trials for 2000/01 season. (2001) Mbwaga, A M.

Integrated management of *Striga* species of cereal crops in Tanzania: Preliminary study of farmer perceptions of soil resources in Central, Lake and Eastern zones (2001) Lamboll R, Hella J, Riches C, Mbwaga A & Ley J.

Acknowledgement

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ABSTRACT

Four cultivars of sorghum (*Sorghum bicolor* (L.) Moench cvs. Pato, P9405, P9406 and Macia) were evaluated for tolerance to infection by the hemiparasitic witchweed *Striga hermonthica* (Del.) Benth., grown under controlled environmental conditions with differing nitrogen (N) availabilities (0.25, 0.5 and 1 mM N as ammonium nitrate). Cultivars differed in susceptibility to *Striga*, using stem biomass as a sensitive indicator of response, with infected Pato exhibiting the greatest depression in stem biomass (84.8 % after 85 d) and P9406 showing the least depression (47.7 %) at higher N availability. Cultivars P9405 and Macia also showed greater tolerance than cv. Pato, with infected P9405 performing consistently well at all nitrogen availabilities. Depression in stem biomass was exacerbated by nutrient limitation (e.g. loss in stem biomass of 86.9 % for P9406 at 0.25 mM N). When uninfected, absolute biomass of Pato was much higher than the other cultivars (between 8.8 – 17.2 g higher for the nutrient treatments imposed), but when infected all cultivars attained equivalent total biomass at final harvest (i.e. ~17 g with 1 mM N). These results indicate that P9406 has the greatest tolerance of *Striga* at higher N availabilities, with P9405 having the most consistent response to *Striga* infection where N supply is variable, in terms of losses in stem biomass on infection.

INTRODUCTION

Striga (Scrophulariaceae) is a genus of hemiparasitic weeds infecting the roots of mainly grasses (Poaceae) in the semi-arid tropics; *S. asiatica* (L.) Kuntze and *S. hermonthica* (Del.) Benth. (Fig. 1, front cover) being two of the most economically detrimental species in sub-Saharan Africa (see Boone *et al.* 1995). Due to the extreme fecundity of these species (thousands of seeds per fruit) and the persistence of seeds in the soil seed bank for many seasons (Worsham 1987), *Striga* infestation is difficult to eradicate. Additionally, major damage is done by the parasite before the aerial parts have emerged above ground, and traditional management practices have a negligible impact once areas become highly infested (see Eplee and Norris [1993] for review). Thus, the most effective control measure is the use of crop varieties that are either resistant to initial *Striga* infection, or which tolerate *Striga* and produce acceptable yields despite infection. Recent research has therefore concentrated on the breeding and testing of resistant/tolerant cultivars of cereals such as *Sorghum bicolor* (L.) Moench (sorghum) and *Zea mays* L. (maize).

Figure 1. *Striga hermonthica* parasitising sorghum in Tanzania, with taller millet visible in the background.

The present study aims to compare the growth of four sorghum cultivars thought to have a high degree of tolerance to *Striga* infection. These include cultivars P9405 and P9406, which were bred for low germination stimulant production at Purdue University (Indiana, USA) and show low levels of infection with both *Striga asiatica* and *S. hermonthica* when compared to a susceptible check (cv. Shanqui Red). Pato and Macia are release varieties in Tanzania. However, Macia is favoured by smallholder farmers for a broad range of traits including pest/disease resistance and the ability to withstand drought (Lamboll *et al.* 2001). Agricultural soils in Tanzania have very low nitrogen availability (Pierce *et al.*, unpublished data). High nitrogen availability has been shown to suppress *Striga* germination and attachment (Cechin and Press 1993), possibly by lowering the production or exudation of germination stimulant produced by the host, and also to lessen the impact of infection on subsequent growth. Indeed,

field trials demonstrate that addition of farmyard manure (FYM) to soils decreases numbers of emerged *Striga* plants and increases grain yield (A.M. Mbwaga, unpublished data). However, FYM is not consistently available to smallholder farmers. Tolerance is therefore critical in conditions of low nitrogen availability, in which differences in host photosynthetic metabolism are also more apparent (Cechin and Press 1993).

Here we investigate the effect of nitrogen availability on the growth and photosynthetic metabolism of the sorghum cultivars detailed above, both uninfected and parasitised by *Striga hermonthica*. Plants were grown under controlled environmental conditions in sand culture, in which nutrient addition was precisely managed. No yield data is presented as grains do not consistently fill in this system (A.L. Gurney, pers. comm.), but altered physiology and phenotype are more readily attributable to nutrient availability in these controlled conditions, than in the field situation.

METHODS

Cultivation

Plants were grown in sand culture in controlled environmental conditions. Two litre pots were lined with nappy liner (Boots Plc., Nottingham, UK) to retain sand, and partially filled with washed silver sand. Seed of *Striga hermonthica* (35 mg, ~3000 seeds; seed from Kibos, Kenya, collected in August 1997) mixed with sand was placed in the pots at 5 cm depth, and then filled with sand (uninfected control pots were entirely filled with sand). Plants were grown at a day/night temperature of 28/22 ºC and relative humidity (RH) of 70/50 %, with water supplied via an automated irrigation system. After 7 d, sorghum cultivars Pato, P9405, P9406 and Macia were assigned to pots according to a randomised block design, with two caryopses of a particular cultivar placed in each pot and covered by sand to a depth of 1 cm. Pots were then supplied with 40 % Long Ashton nutrient solution modified to provide nitrogen at either 0.25, 0.5 or 1 mM N as ammonium nitrate (NH_4NO_3; Hewitt 1966). Following establishment (10 days after planting [dap]) sorghum seedlings were thinned to one per pot. Sorghum was grown at a light intensity (photosynthetic photon flux density [PPFD]) of ~500 µmol m^{-2} s^{-1} at plant height with a 12 h photoperiod.

Continuous measurements

At weekly intervals the height of the youngest visible ligule above the sand surface was measured using a metre rule.

Leaf photosynthetic characteristics

At 58 dap photosynthetic capacity and chlorophyll fluorescence characteristics of the youngest fully expanded leaf (YFEL) of sorghum plants were determined in concert. Plants were first dark-adapted for a minimum of 30 min. An area of leaf blade two-thirds along the length of the YFEL was then placed in a PLC3 leaf cuvette (ADC Bioscientific), connected by fibre optic to both an actinic light source and a PAM-101 modulated chlorophyll fluorometer (H. Walz, Effeltrich, Germany). Chlorophyll fluorescence quenching analysis was conducted using the saturated pulse method detailed by Bolhàr-Nordenkampf and Öquist (1993), and electron transport rate (ETR) calculated as detailed by Maxwell and Johnson (2000). Gas-exchange was measured via infrared gas analysis (IRGA) in the differential mode using an LCA4 (ADC Bioscientific, Hoddesdon, Herts., UK) at a saturating PPFD of 2400 µmol m^{-2} s^{-1}, a temperature of 25 ºC, 60 % RH, a pCO_2 of 360 µmol mol^{-1}, and a flow rate of 360 ml min^{-1}.

Leaf mineral content

Immediately following determination of photosynthetic characteristics, leaf discs were taken from the YFEL and dried at 70 ºC for 3 d. Leaf discs were subsequently digested via the Kjeldahl method (see Hind 1993), and nitrogen and phosphorus concentration determined spectrophotometrically via flow injection analysis, with a Tecator 5012 Analyzer and a 5042 detector (Now Foss, UK).

Leaf chlorophyll content

Chlorophyll content of the YFEL of each sorghum plant was measured using a SPAD-502 chlorophyll meter (Minolta, Japan), calibrated for each cultivar by direct determination of chlorophyll content for six representative leaves. These were extracted in 80 % acetone, absorptance measured at 646 and 663 nm, and total chlorophyll content calculated using the equations of Lichtenthaler and Wellburn (1983).

Biomass

At 85 dap the number of *Striga* shoots visible above ground was recorded, and then sorghum roots washed of sand. The number of *Striga* individuals attached to the roots of each sorghum

plant was also recorded, and then parasites separated from the host. Host plants were divided into root, pseudostem (true stem and leaf sheaths), dead/senescent leaf material and green leaf material. All plant parts were then bagged separately, dried at 70 ºC for 3 d, and subsequently weighed. Instantaneous specific leaf area (SLA; m^2 g^{-1}) was calculated from leaf discs of known area and dry weight.

RESULTS

Continuous measurements

Control plants of sorghum cultivar Pato attained the greatest height of the cultivars tested, achieving 756 cm after 85 d of growth at 1 mM N (cf. 330 – 411 cm in other cultivars; Fig. 2). All cultivars were markedly shorter on infection, and reached approximately the same absolute height of ~200 cm at 1 mM N, with lower nitrogen availability resulting in shorter plants irrespective of *Striga* infection (Fig. 2). Pseudostem length of infected hosts, as a proportion of that of control plants, was greatest in cultivar P9406 at 1 mM N (73.8 % at 85 dap), but was less apparent at lower N availabilities (e.g. 49.6 % at 0.5 mM N; Fig. 3). Cultivars P9405 and Macia also showed less response to infection in terms of plant height than did cv. Pato, in which pseudostems of infected plants were only 26.6 % of uninfected plants at 85 dap (Fig. 3).

Biomass

The relative size of representative plants of each cultivar and each treatment is illustrated in Fig. 4. *Striga* infection decreased whole plant biomass for all cultivars, and increased nitrogen availability resulted in increased total biomass for all cultivars (Fig. 5). Biomass of roots and leaves (both senescent and green portions) were not affected by *Striga* infection, with pseudostem biomass accounting for differences in whole plant biomass. This was reflected by higher root:shoot ratios for all cultivars and at all nitrogen availabilities (Fig. 6). Pseudostems of infected Pato attained only 15.2 % the dry weight of uninfected control plants at 1 mM N (Fig. 7), whereas pseudostems of infected P9406 achieved 52.3 % (although values for this cultivar were 13.1 and 13.9 % at lower nitrogen availabilities). Pseudostems of infected P9405 attained between 24.8 and 27.5 % the dry weight of control plants (Fig. 7). Macia exhibited decreased pseudostem dry weight in response to lower nitrogen availability, but with pseudostems of infected plants being 21.2 % the biomass of controls at 1 mM N, appeared more tolerant to *S. hermonthica* than Pato. The effects of *Striga* infection on

pseudostem biomass were mediated by higher N availability ($p < 0.05$ for all cultivars), particularly so for P9406 ($f = 4.38$, $p = 0.024$). Specific leaf area (SLA) was not affected by any of the treatments (Fig. 8).

Photosynthetic characteristics

Photosynthetic capacity (A_{max}) of all cultivars was relatively low (i.e. <11 µmol m^{-2} s^{-1}; Fig. 4); particularly so at lower nitrogen availability in the case of Pato, Macia and uninfected P9405 (Fig. 9). However, *Striga* infection resulted in significantly ($p \leq 0.05$) lower photosynthetic capacity only in cv. P9405 at higher nitrogen availability (1 mM N), with only non-significant trends apparent in Macia and P9406 at 0.25 mM N (Fig. 9). Photosynthetic electron transport rates (ETR) in the range 32.7 ± 2.9 to 66.1 ± 5.3 µequiv. m^{-2} s^{-1} were not significantly altered by *Striga* infection for any cultivar (Fig. 10). The efficiency of photosystem II (F_v/F_m) was low for all cultivars in all treatments (i.e. between 0.68 to 0.81), but no significant differences were apparent on *Striga* infection or with different nitrogen availability (Fig. 11). Evapotranspiration rates (EvT) showed no difference between treatments except for cultivar P9405, in which uninfected plants at 1 mM N had significantly higher values (Fig. 12).

Foliar mineral content

Mean foliar N contents were extremely low, in the range 8.5 to 20.8 mg g^{-1} (Fig. 13), and P contents in the range 2.1 to 4.4 mg g^{-1} (Fig. 14). N contents were higher on infection for Pato at all nitrogen availabilities, and at 1 mM N for cultivar Macia ($p \leq 0.05$). P contents were higher on infection only for cultivar P9406 (Fig. 14). N or P availability did not significantly alter the foliar contents of these minerals for any cultivar ($p > 0.05$).

Foliar chlorophyll content

Striga infection or nitrogen availability did not affect leaf chlorophyll contents of P9406 or Macia ($p \leq 0.05$). However, *Striga* infection increased chlorophyll content of P9405 and increased chlorophyll content of Pato when more nitrogen was available (Fig. 15).

Striga

The number of *Striga* individuals attached to sorghum roots was highly variable, with no difference between nitrogen treatments for any cultivar excepting that between 0.25 and 0.5 mM N for Macia. *Striga* numbers tended to be lowest at the higher nitrogen availability

(1 mM N), although this was not statistically significant for any cultivar (i.e. $p > 0.05$; Fig. 16). *Striga hermonthica* plants excised from the roots of certain individual sorghum plants are presented in Fig. 17.

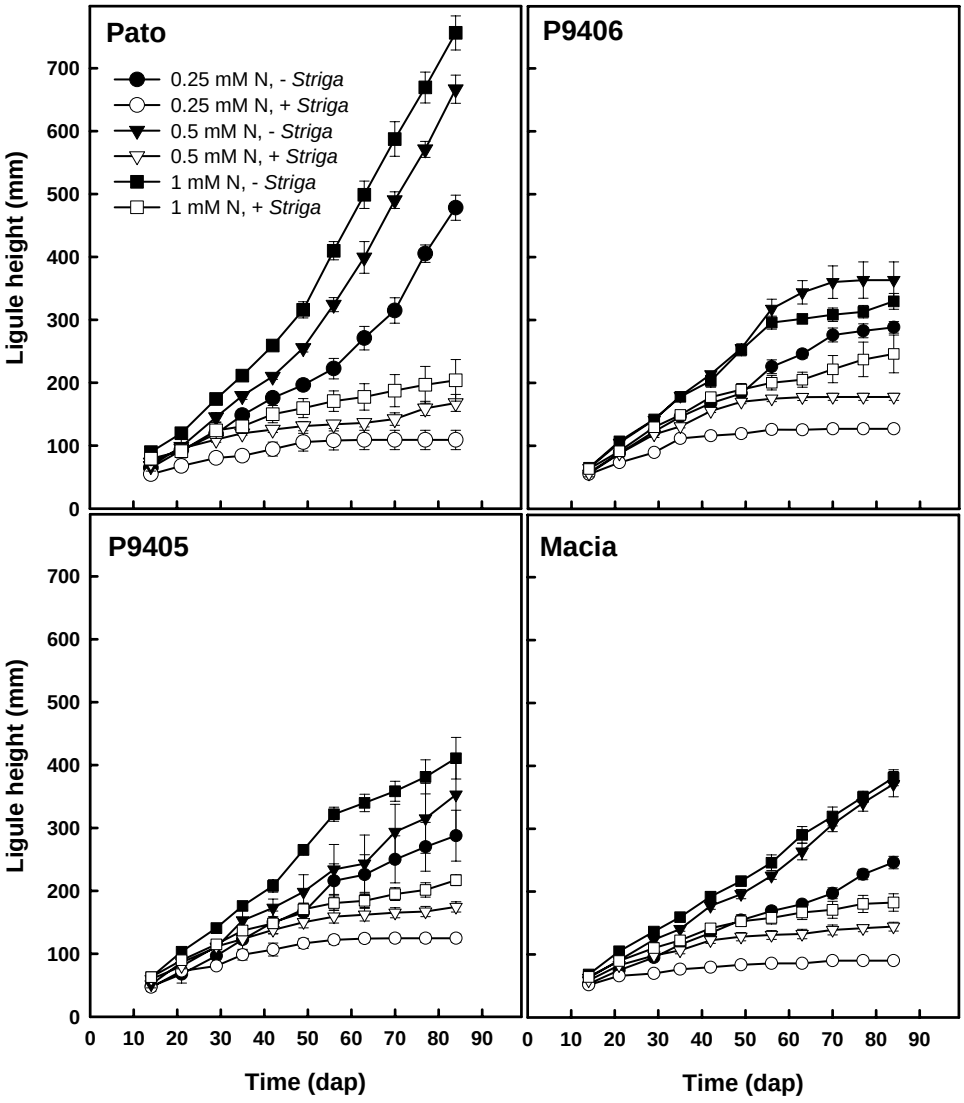

Figure 2. Pseudostem length (height to the youngest visible ligule) of *Sorghum bicolor* cultivars Pato, P9406, P9405 and Macia, either with (+; open symbols) or without (-; closed symbols) infection by *Striga hermonthica* under conditions of different nitrogen availability (0.25, 0.5 or 1.0 mM N as ammonium nitrate). Data represent the mean ± 1 S.E. of six replicates.

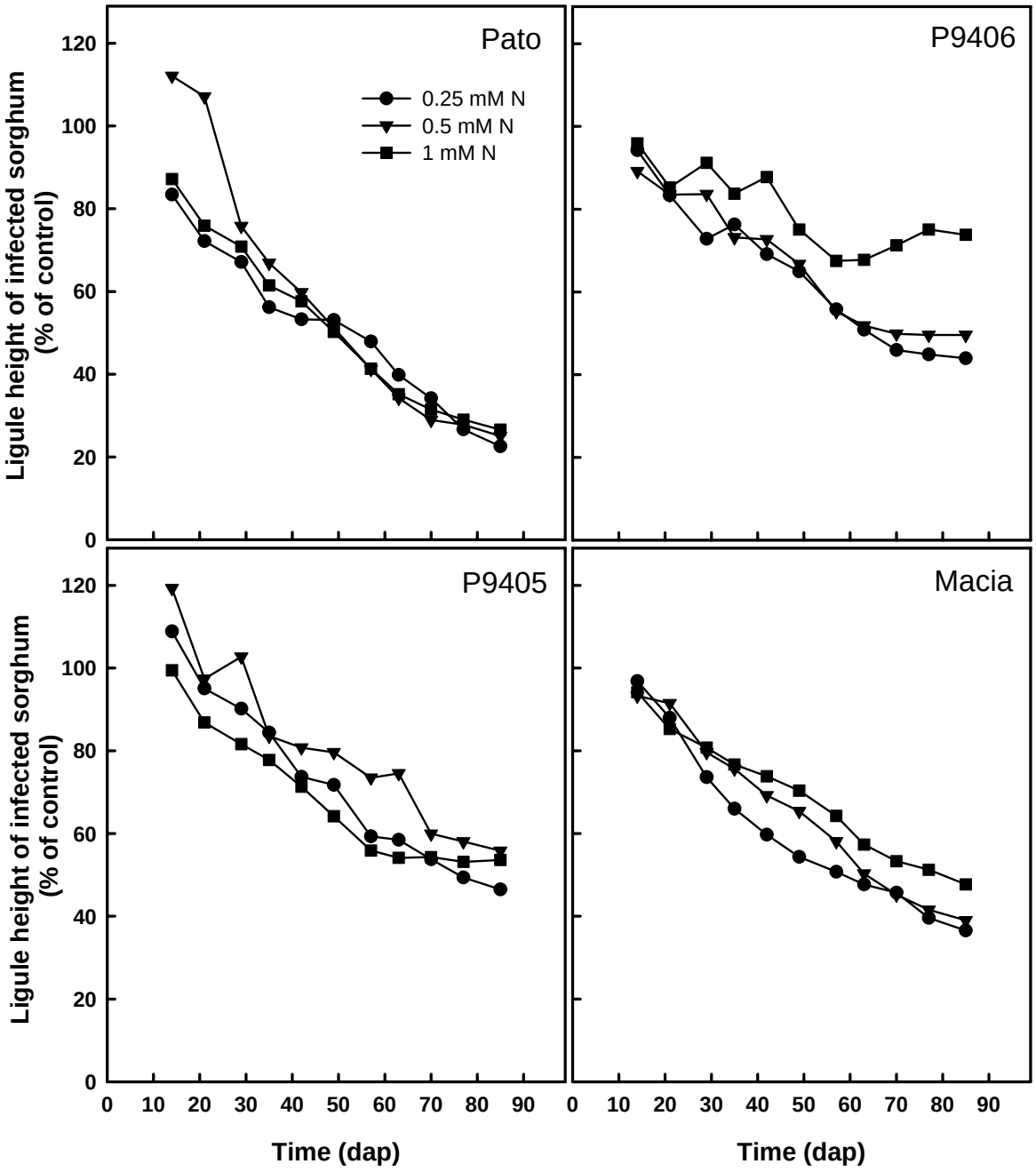

Figure 3. Height to the youngest visible ligule of *Sorghum bicolor* cultivars Pato, P9406, P9405 and Macia infected by *Striga hermonthica* (as a proportion of uninfected control plant height) under conditions of different nitrogen availability (0.25, 0.5 or 1.0 mM N as ammonium nitrate). Data represent the mean of six replicates.

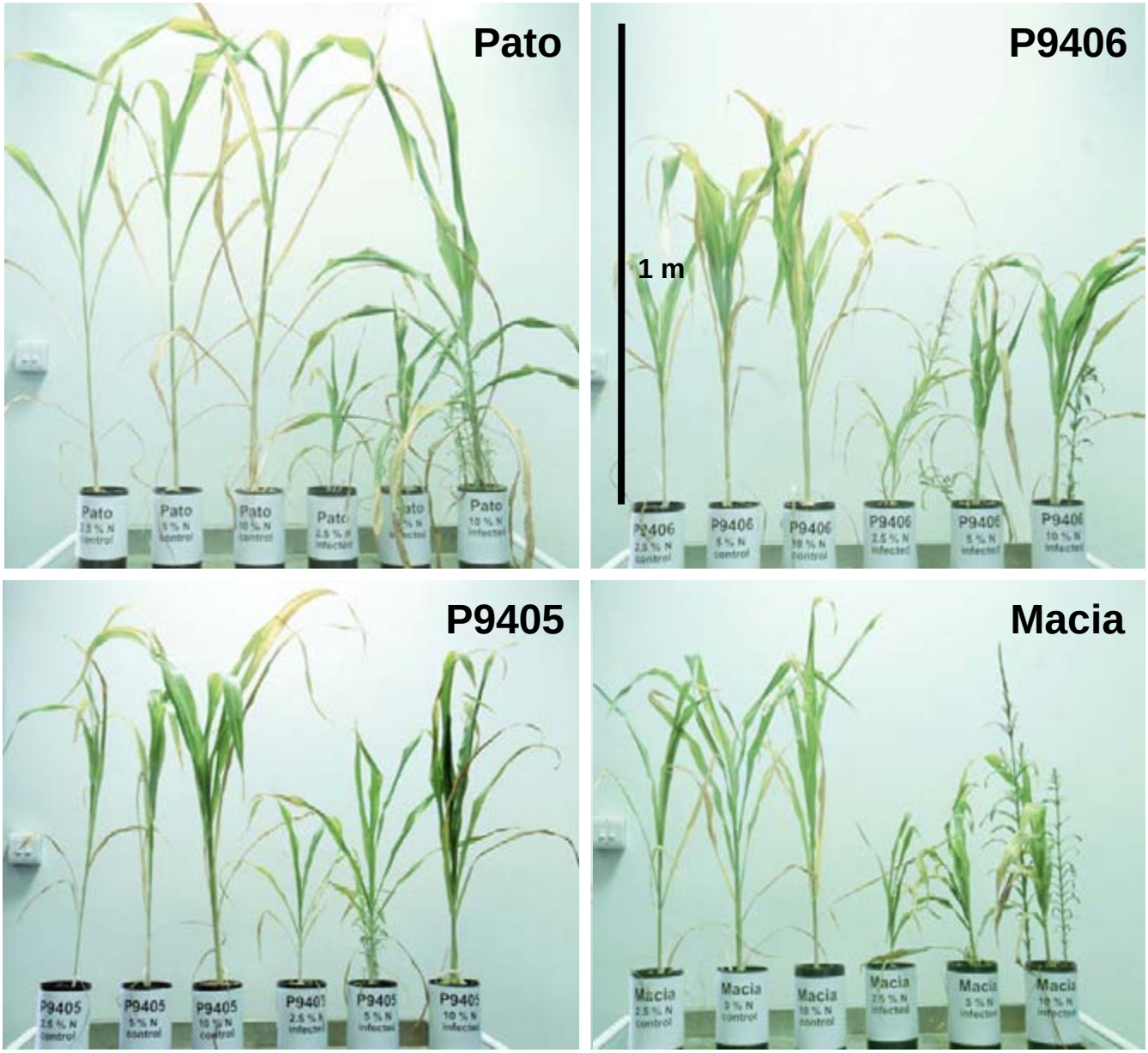

Figure 4. Representative individuals of each cultivar of *Sorghum bicolor* (Pato, P9406, P9405 and Macia) and of each treatment (uninfected control or infected with *Striga hermonthica*; 0.25, 0.5 and 1.0 mM N) at 80 days after planting (dap).

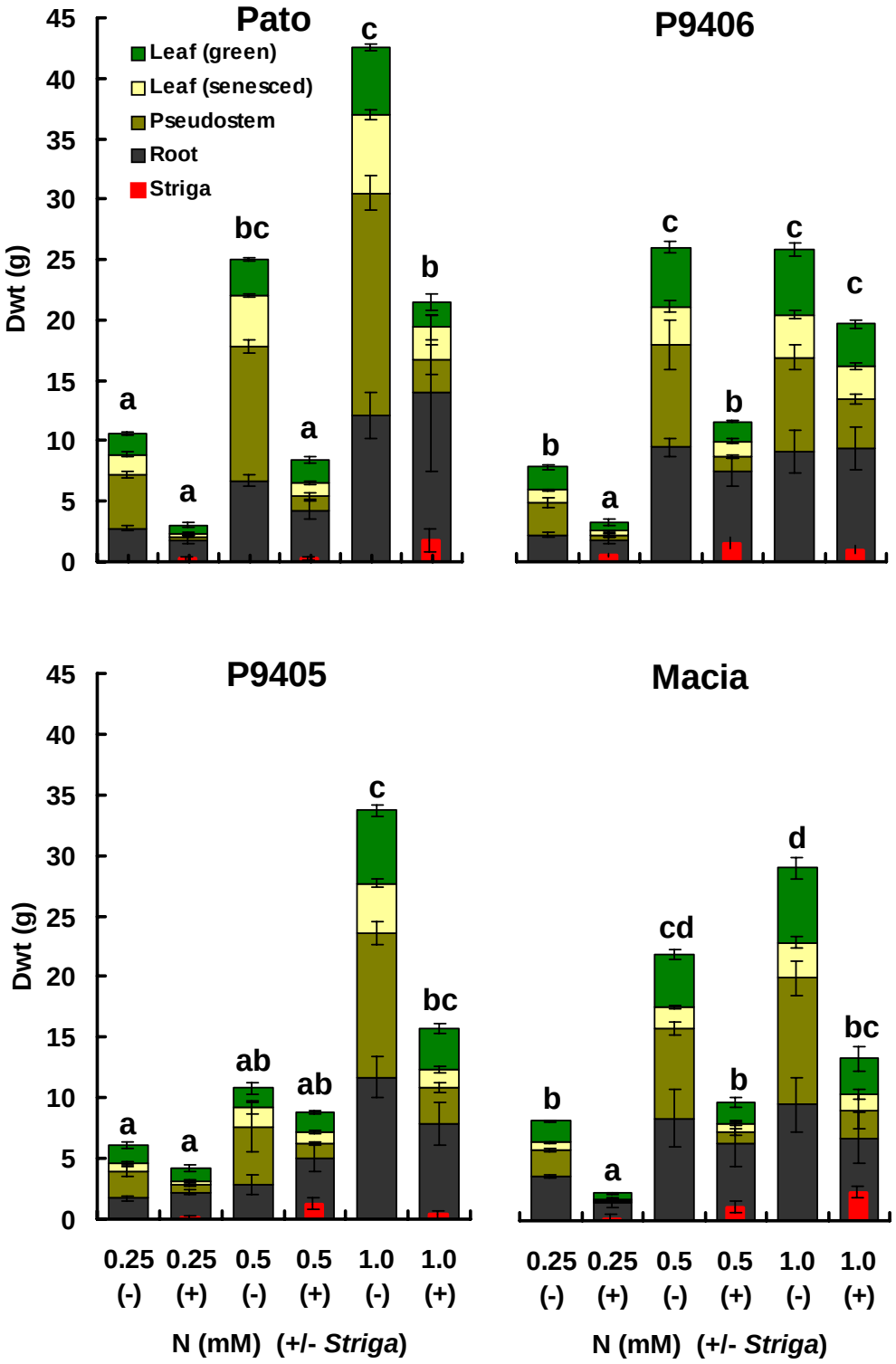

Figure 5. Biomass (g dry weight) of organs (root, pseudostem, dead/senescent leaf, green leaf) comprising *Sorghum bicolor* cultivars Pato, P9406, P9405 and Macia at 85 dap, either with (+) or without (-) infection by hemiparasitic *Striga hermonthica* and under conditions of different nitrogen availability (0.25, 0.5 or 1.0 mM N as ammonium nitrate). Red bars represent biomass of *S. hermonthica* within each treatment. Data represent the mean ± 1 S.E. of six replicates. Different letters indicate significant differences in total plant dry weight between treatments within each cultivar at the $p \leq 0.05$ level as determined by Tukey's multiple comparison procedure (ANOVA).

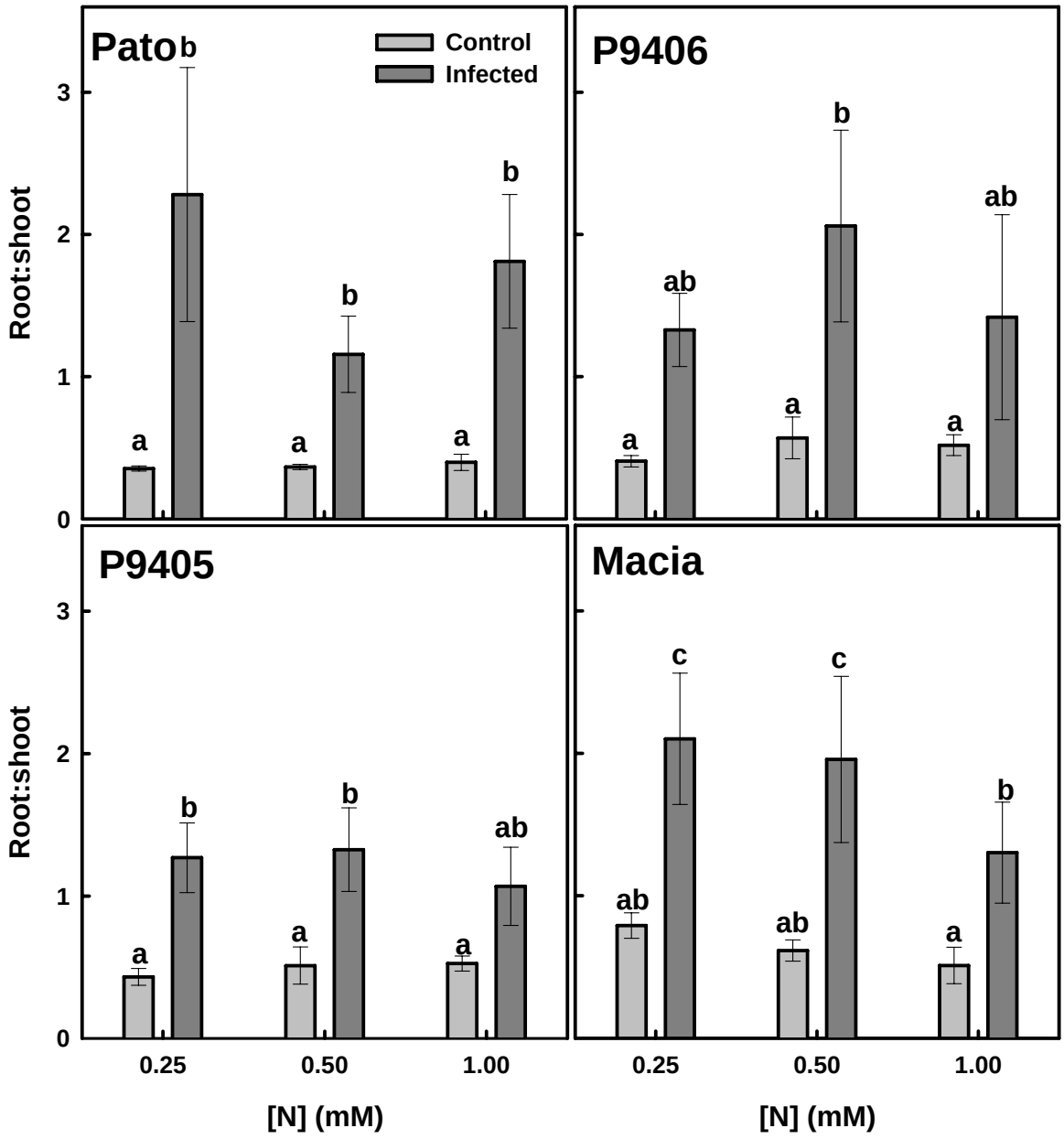

Figure 6. Root:shoot ratio of *Sorghum bicolor* cultivars Pato, P9406, P9405 and Macia at 85 dap, either with or without infection by hemiparasitic *Striga hermonthica* and under conditions of different nitrogen availability (0.25, 0.5 or 1.0 mM N as ammonium nitrate). Data represent the mean ± 1 S.E. of six replicates. Different letters indicate significant differences between treatment means within each cultivar at the $p \leq 0.05$ level as determined by Tukey's multiple comparison procedure (ANOVA).

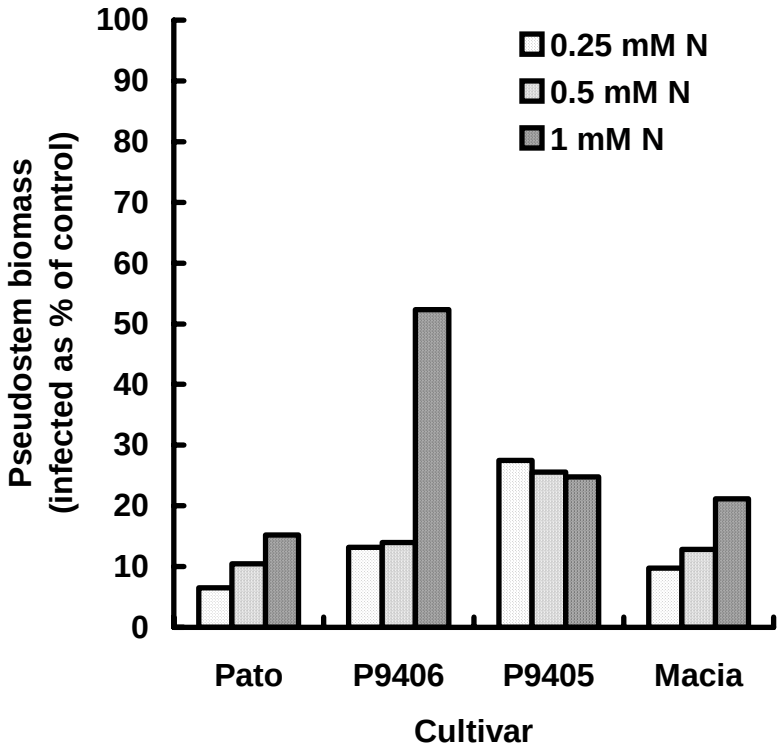

Figure 7. Pseudostem biomass of infected *Sorghum bicolor* (cultivars Pato, P9406, P9405 and Macia) as a proportion of uninfected control plants at 85 dap, under conditions of different nitrogen availability (0.25, 0.5 or 1.0 mM N as ammonium nitrate). Data represent the mean of six replicates.

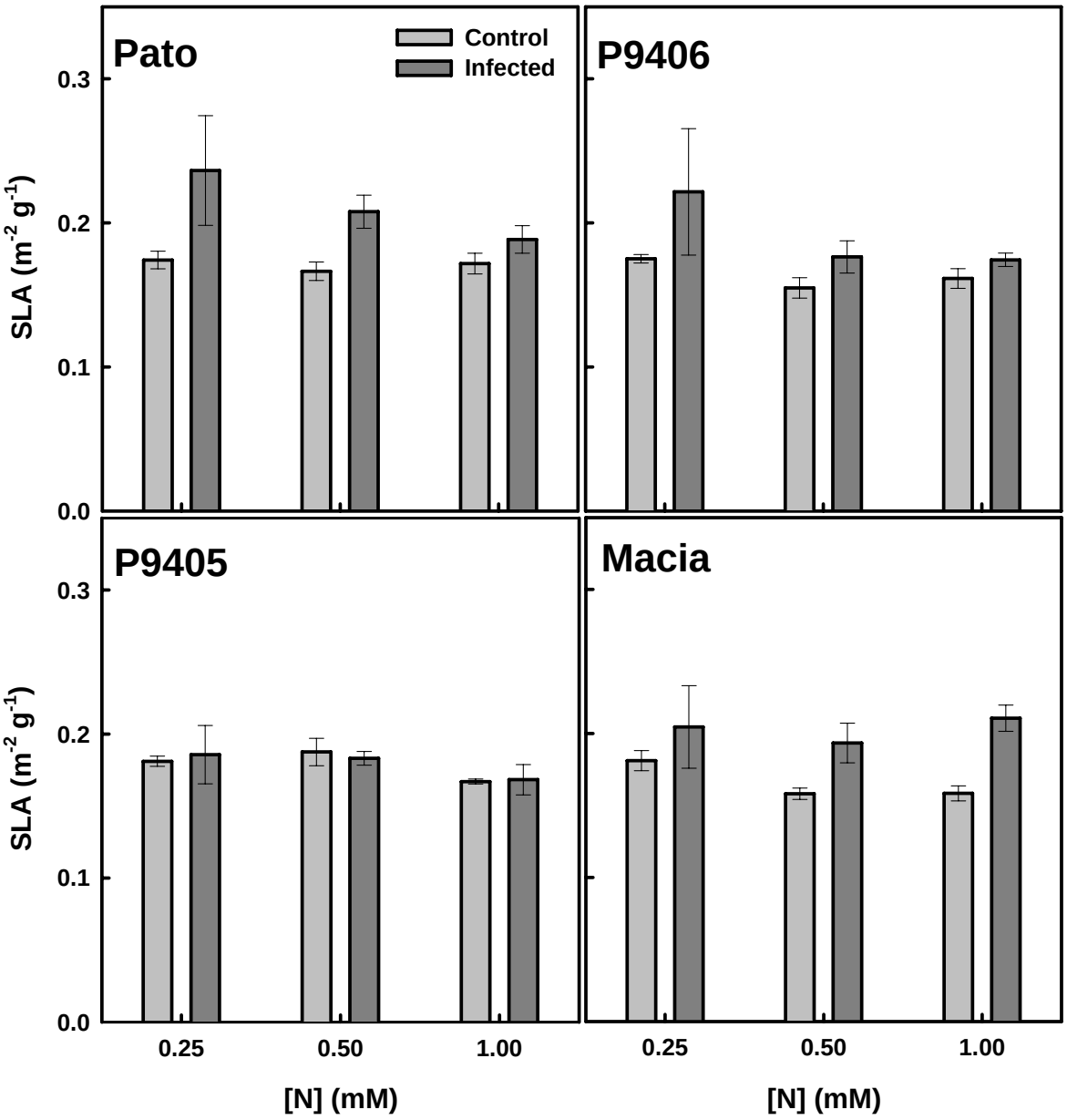

Figure 8. Specific leaf area of *Sorghum bicolor* cultivars Pato, P9406, P9405 and Macia at 85 dap, either with or without infection by hemiparasitic *Striga hermonthica* and under conditions of different nitrogen availability (0.25, 0.5 or 1.0 mM N as ammonium nitrate). Data represent the mean ± 1 S.E. of six replicates. No significant differences between treatment means were determined within each cultivar at the $p \leq 0.05$ level as determined by ANOVA.

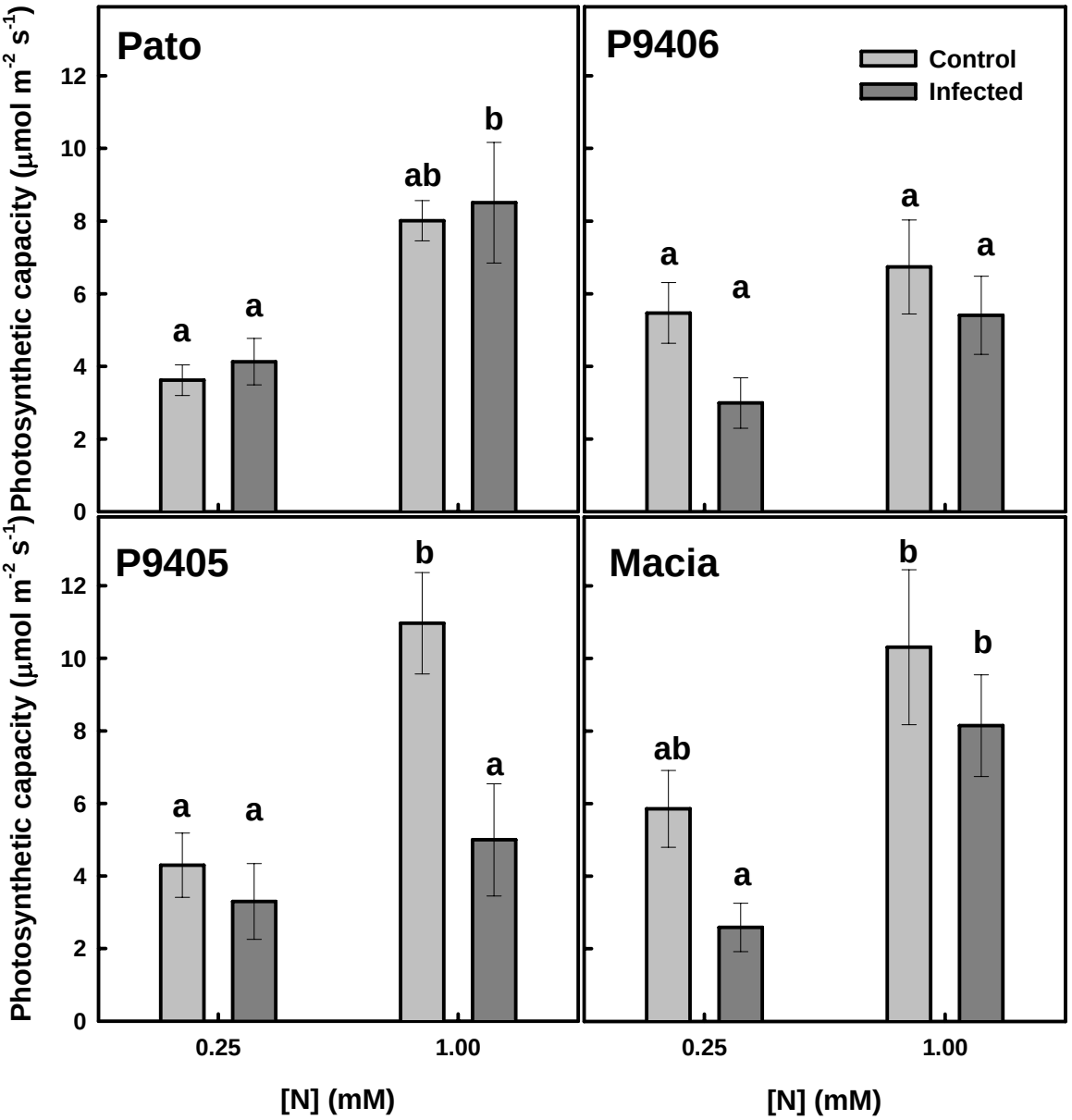

Figure 9. Photosynthetic capacity of *Sorghum bicolor* cultivars Pato, P9406, P9405 and Macia at 58 dap, under a saturating PPFD of 2400 µmol m^{-2} s^{-1}. Plants were grown either with or without infection by *Striga hermonthica* and under conditions of different nitrogen availability (0.25 or 1.0 mM N as ammonium nitrate). Data represent the mean ± 1 S.E. of six replicates. Different letters indicate significant differences between treatment means within each cultivar at the $p \leq 0.05$ level as determined by Tukey's multiple comparison procedure (ANOVA).

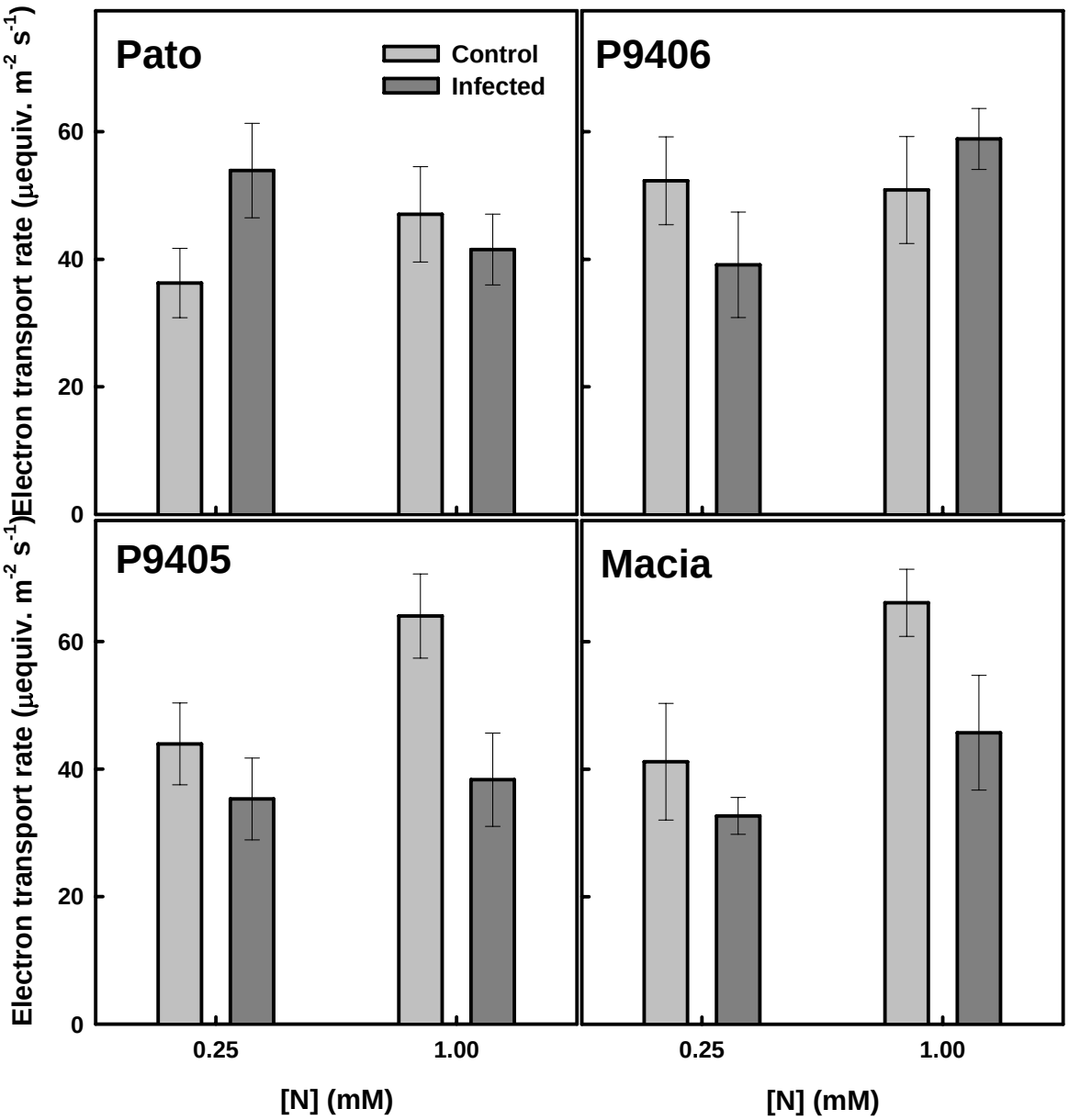

Figure 10. Photosynthetic electron transport rate of *Sorghum bicolor* cultivars Pato, P9406, P9405 and Macia at 58 dap, at growth PPFD of 300 µmol m^{-2} s^{-1}. Plants were grown either with or without infection by hemiparasitic *Striga hermonthica* and under conditions of different nitrogen availability (0.25 or 1.0 mM N as ammonium nitrate). Data represent the mean ± 1 S.E. of six replicates. No significant differences between treatment means within each cultivar were detected at the $p \leq 0.05$ level (ANOVA).

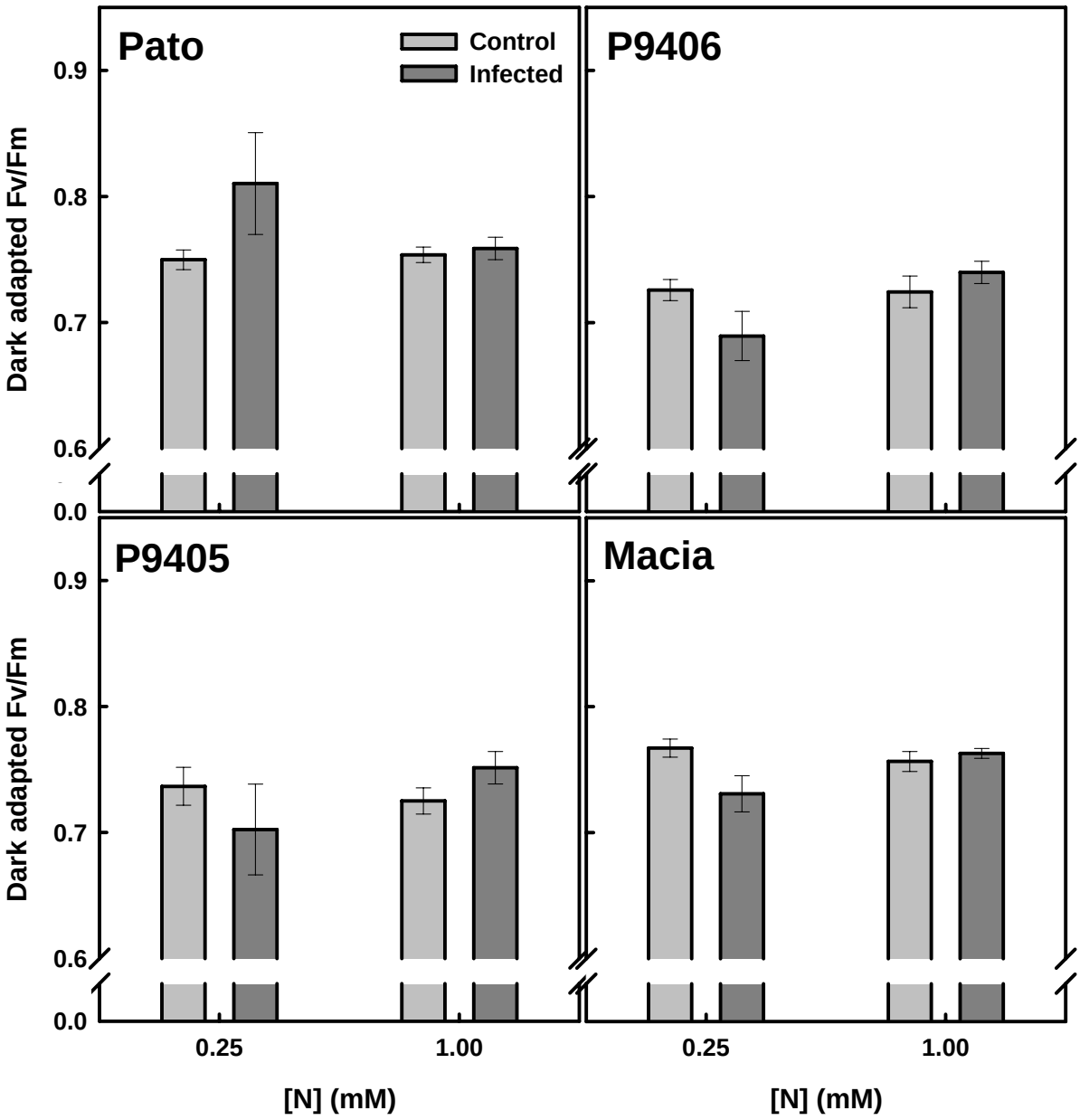

Figure 11. Dark adapted F_v/F_m of *Sorghum bicolor* cultivars Pato, P9406, P9405 and Macia at 58 dap, either with or without infection by hemiparasitic *Striga hermonthica* and under conditions of different nitrogen availability (0.25 or 1.0 mM N as ammonium nitrate). Data represent the mean ± 1 S.E. of six replicates. No significant differences between treatment means within each cultivar were detected at the $p \leq 0.05$ level (ANOVA).

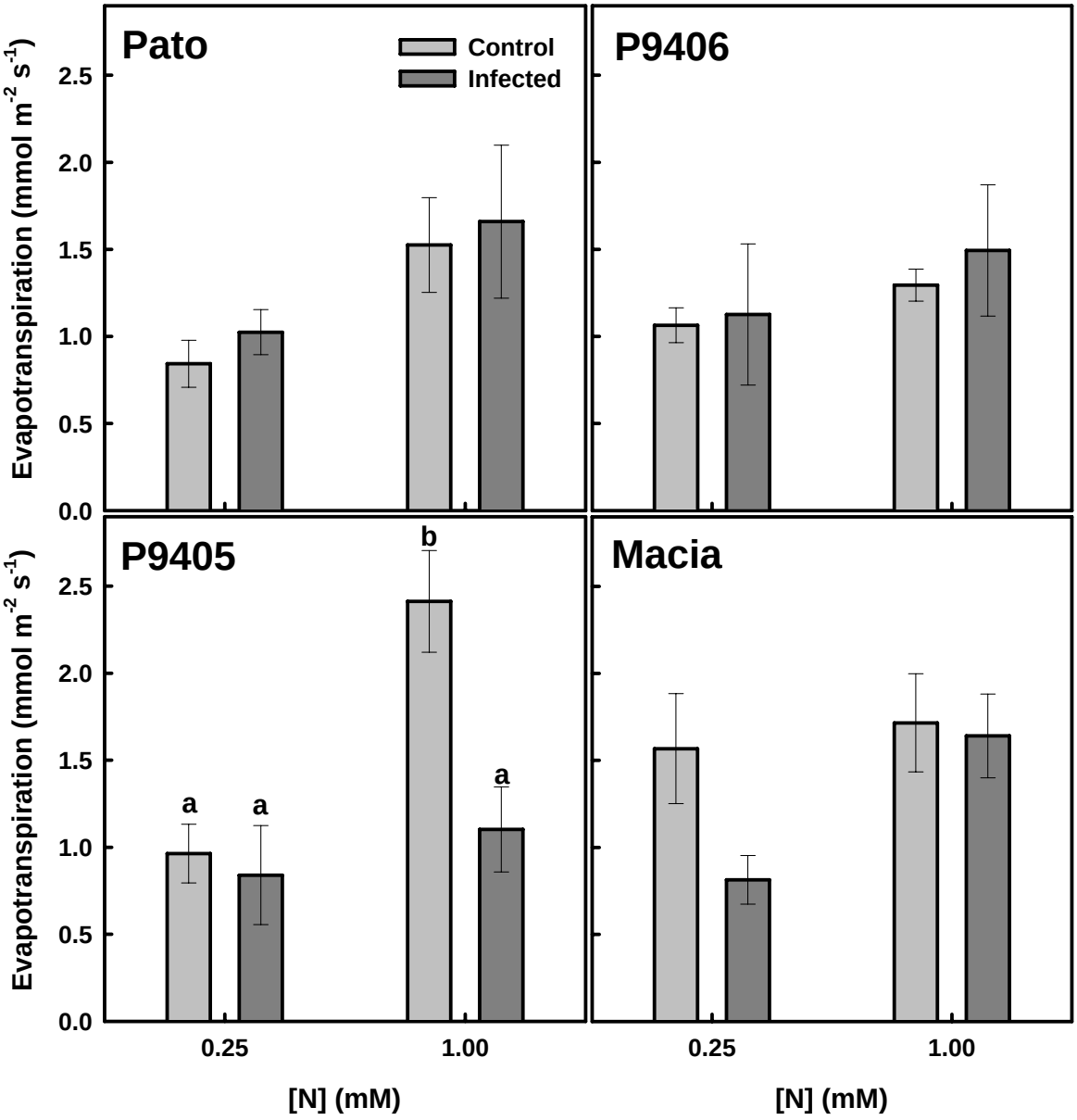

Figure 12. Evapotranspiration rate of *Sorghum bicolor* cultivars Pato, P9406, P9405 and Macia at 58 dap, either with or without infection by hemiparasitic *Striga hermonthica* and under conditions of different nitrogen availability (0.25 or 1.0 mM N as ammonium nitrate). Data represent the mean ± 1 S.E. of six replicates. Different letters indicate significant differences between treatment means within each cultivar at the $p \leq 0.05$ level as determined by Tukey's multiple comparison procedure (ANOVA).

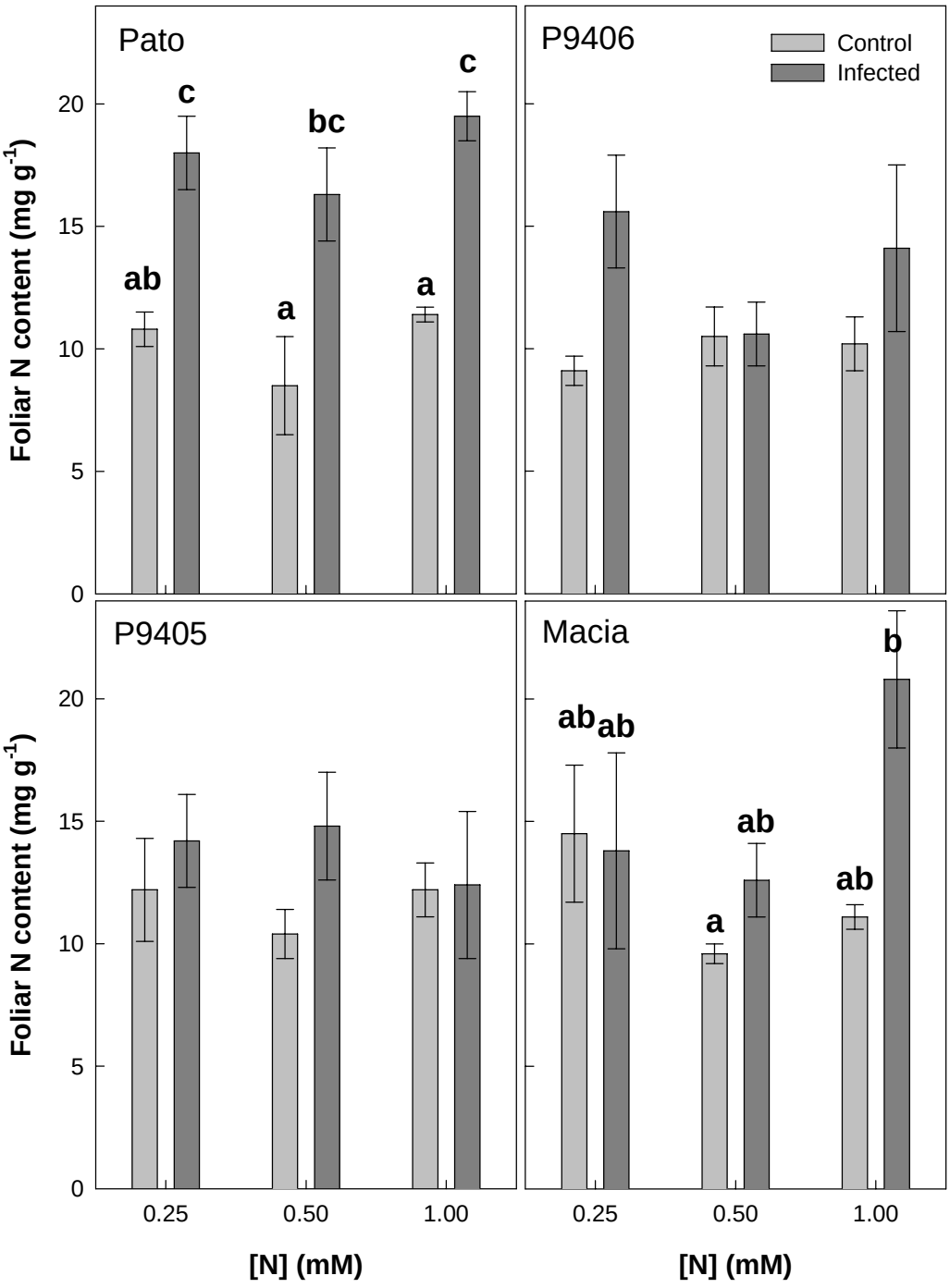

Figure 13. Nitrogen (N) content of the YFEL of *Sorghum bicolor* cultivars Pato, P9406, P9405 and Macia at 58 dap, either with or without infection by hemiparasitic *Striga hermonthica* and under conditions of different nitrogen availability (0.25, 0.5 or 1.0 mM N as ammonium nitrate). Data represent the mean ± 1 S.E. of six replicates. Different letters indicate significant differences between treatment means within each cultivar at the $p \leq 0.05$ level as determined by Tukey's multiple comparison procedure (ANOVA). No significant differences were determined for cvs. P9406 or P9405.

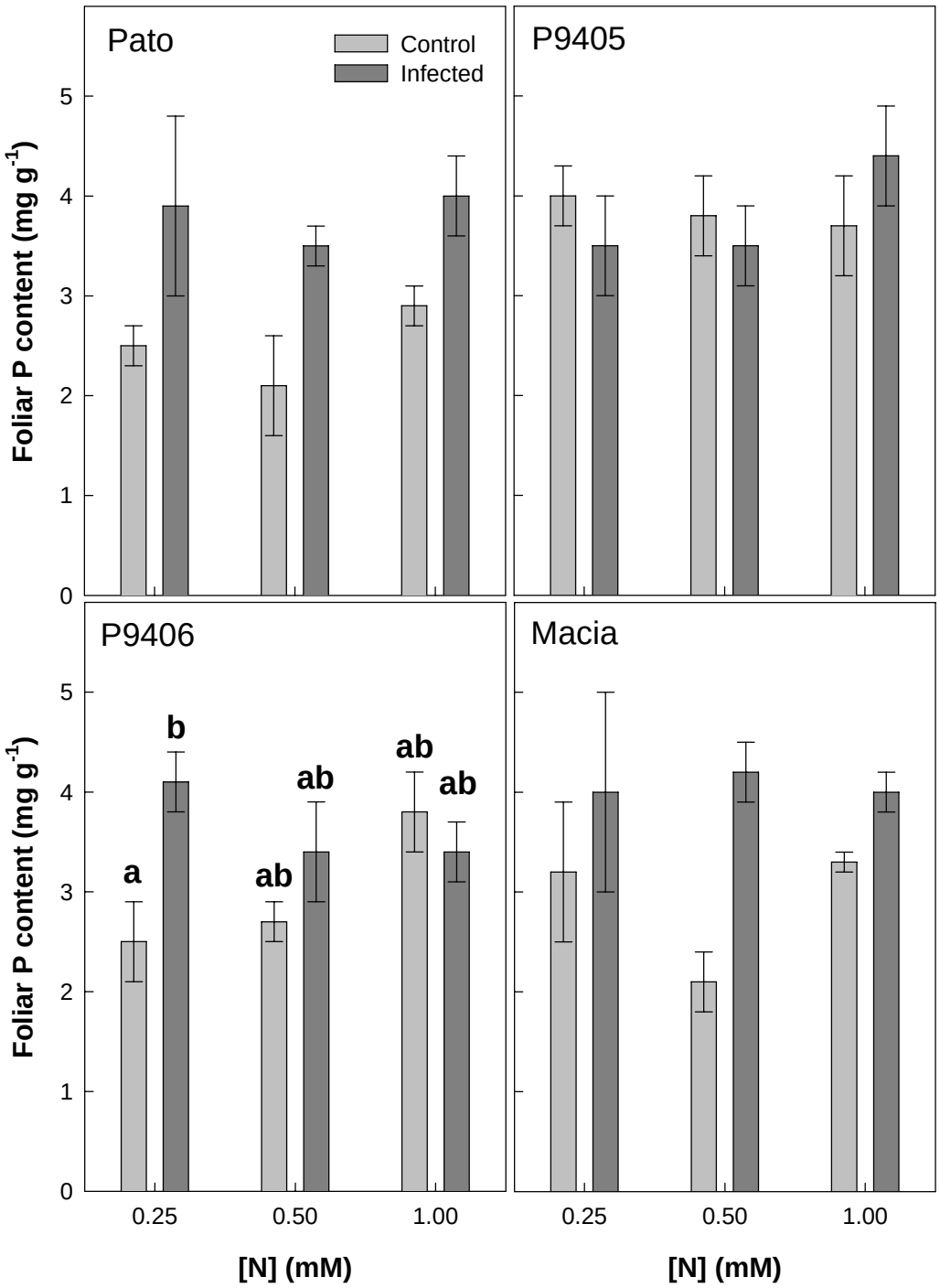

Figure 14. Phosphorus (P) content of the YFEL of *Sorghum bicolor* cultivars Pato, P9406, P9405 and Macia at 58 dap, either with or without infection by hemiparasitic *Striga hermonthica* and under conditions of different nitrogen availability (0.25, 0.5 or 1.0 mM N as ammonium nitrate). Data represent the mean ± 1 S.E. of six replicates. Different letters indicate significant differences between treatment means within each cultivar at the $p \leq 0.05$ level as determined by Tukey's multiple comparison procedure (ANOVA). No significant differences were evident for cvs. Pato, P9405 or Macia.

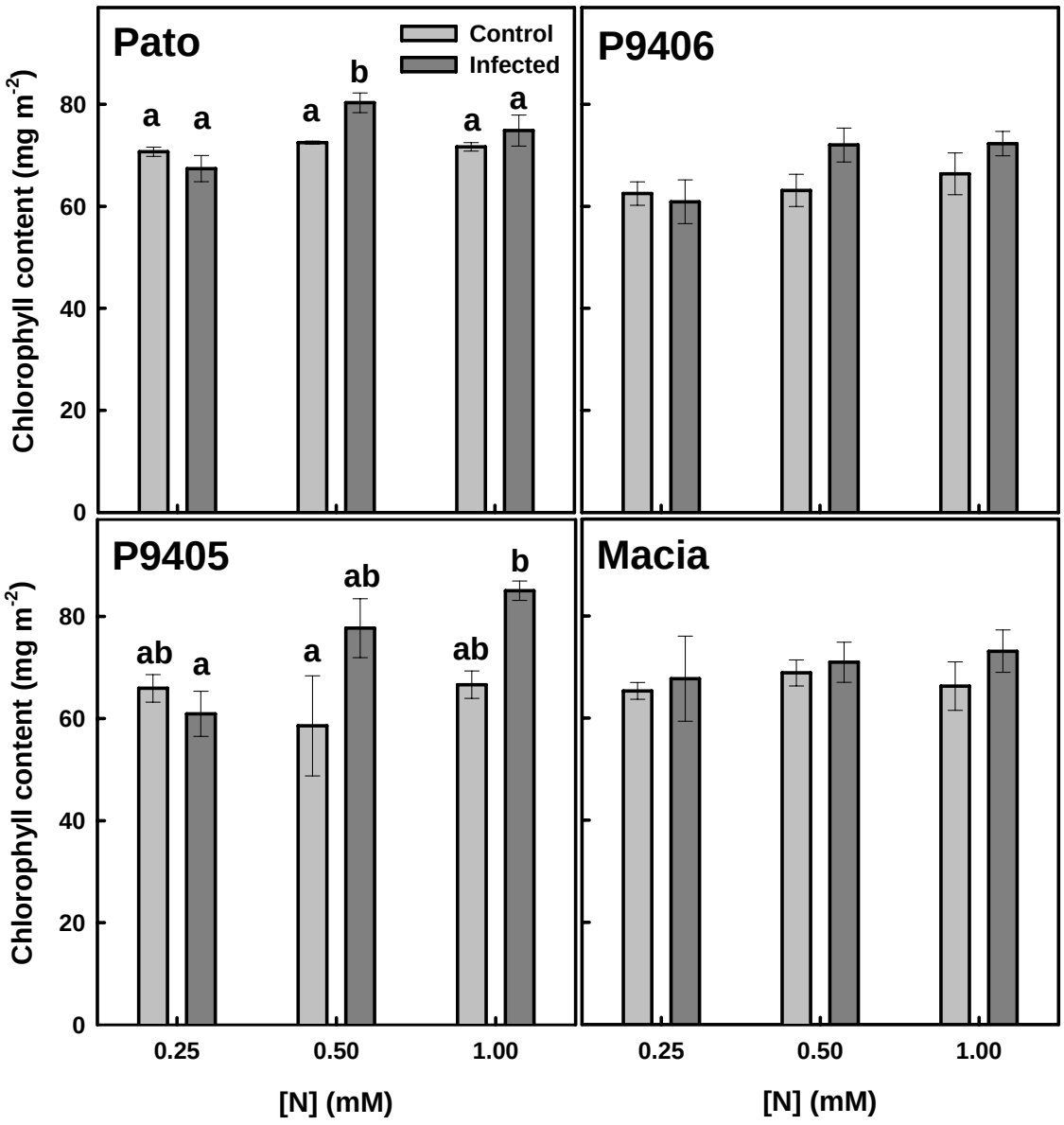

Figure 15. Chlorophyll content of the YFEL of *Sorghum bicolor* cultivars Pato, P9406, P9405 and Macia at 58 dap, either with or without infection by hemiparasitic *Striga hermonthica* and under conditions of different nitrogen availability (0.25, 0.5 or 1.0 mM N as ammonium nitrate). Data represent the mean ± 1 S.E. of six replicates. Different letters indicate significant differences between treatment means within each cultivar at the $p \leq 0.05$ level as determined by Tukey's multiple comparison procedure (ANOVA). No significant differences were evident for cvs. P9406 and Macia.

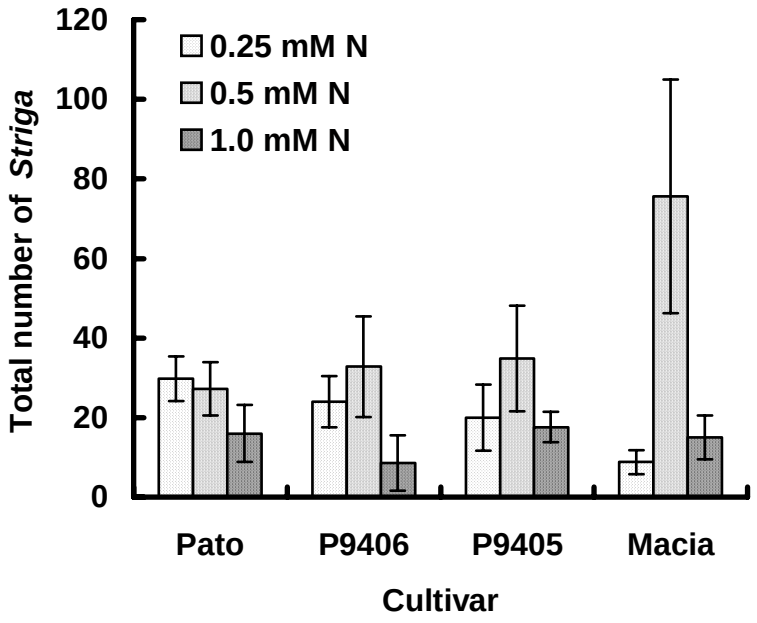

Figure 16. Total number of *Striga hermonthica* individuals parasitising the roots of *Sorghum bicolor* cultivars Pato, P9406, P9405 and Macia at 85 dap, under conditions of different nitrogen availability (0.25, 0.5 or 1.0 mM N as ammonium nitrate). Data represent the mean ± 1 S.E. of six replicates. No significant differences between treatment means within each cultivar where found at the $p \leq 0.05$ level (ANOVA).

Figure 17. *Striga hermonthica* from the roots of individual *Sorghum bicolor* plants (cv. P9406 [**a,c**] and P9405 [**b**]) grown at either 0.5 or 1.0 mM N, at 85 days after planting (dap).

DISCUSSION

Stunting was evident for all sorghum cultivars when parasitised by *Striga hermonthica* (i.e. shorter pseudostems with less biomass, and higher root:shoot ratios), and is a common symptom of *Striga* infection (e.g. Gurney *et al*. 1995) with more tolerant cultivars exhibiting less stunting. Of the four cultivars tested, less extensive stunting for P9406 indicated the greatest tolerance to *Striga* at higher nitrogen availability. However, cultivar P9405 showed a relatively high degree of tolerance throughout a range of nitrogen availabilities. Macia also exhibited characteristics of a tolerant line, performing better than Pato in terms of stunting; the present study supports farmers' perceptions and use of this variety in *Striga* infested areas (Lamboll *et al*. 2001). Use of cultivar P9406 is also particularly recommended, and P9405 shows a consistent response to nitrogen availability and *Striga* infection.

Direct comparison of nutrient application in the field (doses of manure) and in rhizotrons (continuous through-flow of nutrient solution) is not possible. However, foliar N and P values in the lab were similar for the same cultivars grown in the field (i.e. a range of 8.5 – 20.8 mg N g^{-1} d.wt in the lab *c.* 19 – 24 mg N g^{-1} d.wt on luseni soil in the field; Pierce, Ley, Watling *et al*., unpublished data). Leaf phosphorus contents were also similar (2.1 – 4.4 mg P g^{-1} d.wt in the lab *c.* 1.6 – 4.2 mg P g^{-1} d.wt in the field), indicating that plants experienced equivalent nutrient availabilities. Indeed, foliar nutrient content, rather than availability to the roots, is perhaps most critical as N and P directly govern the amount of enzymes that are available to do work within the leaf, and thus metabolic constraints should be similar for field and lab-grown plants.

Stunting was not the result of a general effect on plant growth, with root and leaf biomass remaining largely unchanged, and was associated mainly with changes in pseudostem biomass (see also Graves, Press and Stewart 1989). Small amounts (<0.5 g d.wt.) of *Striga* resulted in stunting (Fig. 12; see also Gurney *et al*. 1999). An ability to maintain photosynthetic rates despite infection is thought to be a characteristic of tolerance (Gurney *et al*. 1995). Indeed, photosynthetic metabolism was not greatly influenced by infection in any cultivar in the present study. Pato exhibited the greatest growth response to infection but showed no response of any measured photosynthetic characteristic at low nitrogen availabilities; i.e. growth response to *Striga* infection was not determined by photosynthetic metabolism. Extremely low photosynthetic rates in uninfected plants suggest that at these low nitrogen availabilities, and low foliar nitrogen contents, nitrogen was the major limitation to

photosynthetic metabolism. Infected P9405 did have lower rates of evapotranspiration associated with lower photosynthetic capacity (*c*. uninfected controls) at 1 mM N, supporting the hypothesis that the effects of *Striga* infection on host photosynthetic metabolism are indirect consequences of limitation by stomatal aperture and consequent internal CO_2 availability. These data support the hypothesis that *Striga* interferes with host growth via a process other than solely the re-allocation of host resources to the parasite. A number of allelopathic (toxic) compounds occur in Scrophulariaceae that could potentially interfere with host metabolism and produce the observed growth response; e.g. iridoid glycosides have now been found in *Striga asiatica* and *S. gesnerioides* (Pierce, Press, Scholes and Jensen, unpublished data), and are plausible candidates for this role.

In conclusion, *Sorghum bicolor* cv. P9406 exhibited particular tolerance to infection by *Striga hermonthica* when compared with cv. Pato under conditions of greater nitrogen availability. Cultivars P9405 and Macia also showed more tolerance than cv. Pato, with a high degree of tolerance exhibited by P9405 even at extremely low nitrogen availability. P9406 is thus particularly recommended for situations in which more nutrients are available, P9405 for a range of soil fertilities (variable soil quality), and Macia provides a further sensible choice for farmers affected by the *Striga* problem. Differences in growth response to infection in these cultivars were not a result of altered photosynthetic metabolism, and future investigation of the cultivar response will concentrate on the possible production of phytotoxic agents by *S. hermonthica*.

LITERATURE CITED

Bolhàr-Nordenkampf HR and Öquist G. 1993. Chlorophyll fluorescence as a tool in photosynthesis research. *In.* Hall DO, Scurlock JMO, Bolhàr-Nordenkampf HR, Leegood RC and Long SP (eds.) Photosynthesis and Production in a Changing Environment. Chapman and Hall. London.

Boone LS, Fate G, Chang M and Lynn DG. 1993. Seed germination. *In.* Press MC and Graves JD (eds.) Parasitic Plants. Chapman and Hall. London.

Cechin I and Press MC. 1993. Nitrogen relations of the sorghum-*Striga* host-parasite association: growth and photosynthesis. *Plant, Cell and Environment* 16: 237-247.

Eplee RE and Norris R. 1993. Control of parasitic weeds. *In.* Press MC and Graves JD (eds.) Parasitic Plants. Chapman and Hall. London.

Graves JD, Press MC and Stewart GR. 1989. A carbon balance model of the sorghum-*Striga* hermonthica host-parasite association. *Plant, Cell and Environment* 12: 101-107.

Gurney AL, Press MC and Ransom JK. 1995. The parasitic angiosperm *Striga hermonthica* can reduce photosynthesis of its sorghum and maize hosts in the field. *Journal of Experimental Botany* 46(293): 1817-1823.

Gurney AL, Press MC and Scholes JD. 1999. Infection time and density influence the response of sorghum to the parasitic angiosperm *Striga hermonthica*. *New Phytologist* 143: 573-580.

Hewitt EJ. 1966. Sand and Water culture Methods used in the study of Plant Nutrition. (2nd edition). London and Reading: Commonwealth Agricultural Bureau. The Eastern Press.

Hind G. 1993. Thylakoid components and processes. *In.* Hall DO, Scurlock JMO, Bolhàr-Nordenkampf HR, Leegood RC and Long SP (eds.) Photosynthesis and Production in a Changing Environment. Chapman and Hall. London.

Lamboll RI, Hella J, Mbwaga AM and Riches C. 2001. *Striga* research activities in Central Zone and Lake Zone of Tanzania: evaluation of on-farm research trials 2000/2001 season. Unpublished Ilonga ARI/NRI project report.

Lichtenthaler HK and Wellburn AR. 1983. Determinations of total carotenoids and chlorophylls *a* and *b* of leaf extracts in different solvents. *Biochemistry Society Transactions* 11: 591-592.

Maxwell K and Johnson GN. 2000. Chlorophyll fluorescence – a practical guide. *Journal of Experimental Botany* 51(345): 659-668.

Worsham AD. 1987. Germination of witchweed seeds. *In.* Press MC and Graves JD (eds.) Parasitic Plants. Chapman and Hall. London.