New Phytologist

Research

Biological limits on nitrogen use for plant photosynthesis: a quantitative revision comparing cultivated and wild species

José L. Rotundo[1] and Pablo A. Cipriotti[2]

[1]Facultad de Ciencias Agrarias, IICAR – UNR/CONICET, Zavalla, Santa Fe, Argentina; [2]Depto. de Métodos Cuantitativos y Sistemas de Información – IFEVA, Facultad de Agronomía, UBA/CONICET, Buenos Aires, Argentina

Author for correspondence:
José L. Rotundo
Tel: +54 0341 4970080
Email: jrotundo@unr.edu.ar

Received: *13 September 2016*
Accepted: *28 October 2016*

New Phytologist (2016)
doi: 10.1111/nph.14363

Key words: carbon sequestration, photosynthesis, photosynthetic nitrogen (N)-use efficiency, primary productivity, Rubisco.

Summary

- The relationship between leaf photosynthesis and nitrogen is a critical production function for ecosystem functioning. Cultivated species have been studied in terms of this relationship, focusing on improving nitrogen (N) use, while wild species have been studied to evaluate leaf evolutionary patterns. A comprehensive comparison of cultivated vs wild species for this relevant function is currently lacking. We hypothesize that cultivated species show increased carbon assimilation per unit leaf N area compared with wild species as associated with artificial selection for resource-acquisition traits.
- We compiled published data on light-saturated photosynthesis (A_{max}) and leaf nitrogen (LN_{area}) for cultivated and wild species. The relationship between A_{max} and LN_{area} was evaluated using a frontier analysis (90th percentile) to benchmark the biological limit of nitrogen use for photosynthesis.
- Carbon assimilation in relation to leaf N was not consistently higher in cultivated species; out of 14 cultivated species, only wheat, rice, maize and sorghum showed higher ability to use N for photosynthesis compared with wild species.
- Results indicate that cultivated species have not surpassed the biological limit on nitrogen use observed for wild species. Future increases in photosynthesis based on natural variation need to be assisted by bioengineering of key enzymes to increase crop productivity.

Introduction

Leaf photosynthesis is the main process of energy capture for the total biosphere (Lange *et al.*, 1987). Understanding ecosystem functioning requires analyzing photosynthesis performance of relevant plant groups from both natural ecosystems and agroecosystems. Light harvesting processes and electron transport, jointly with the enzymatic machinery of carbon (C) metabolism, require large investments in leaf nitrogen (N) in the form of protein (Hohmann-Marriott & Blankenship, 2011). Therefore, N is considered the main limiting nutrient for primary productivity for both agricultural and natural environments (LeBauer & Treseder, 2008). The relationship between leaf N and photosynthesis is a fundamental production-resource function for ecosystem functioning as photosynthesis also provides the energy for heterotrophic consumption (Field & Mooney, 1991; Vitousek *et al.*, 1997). Here we describe the relationship between leaf, light-saturated, photosynthesis (A_{max}; μmol CO_2 m^{-2} s^{-1}) and N per unit leaf area (LN_{area}; g m^{-2}) for cultivated and wild species using a database compiled from previously published data.

Modern agriculture depends on the productivity of a limited set of species (Geps, 2002; Ross-Ibarra *et al.*, 2007). Cultivated and wild species have been independently characterized for their ability to use leaf N for photosynthesis. Research on cultivated species focused on practical aspects related to improved N-use efficiency for higher yield, food security, and reduced pollution (Muchow & Sinclair, 1994; Peng *et al.*, 1995; Dreccer *et al.*, 2000; Cassman *et al.*, 2003). Studies evaluating wild species, on the other hand, have usually tested whether the relationship between A_{max} and LN_{area} reflect evolutionary patterns associated with resource availability and environmental constraints (Field & Mooney, 1991; Poorter & Evans, 1998; Wright *et al.*, 2004, 2005; Hassiotou *et al.*, 2010). Comparing this production function provides a unique opportunity to test whether there has been improvement in the ability to utilize N in cultivated species beyond what is observed for wild species. A comprehensive comparison including major cultivated species upon which human food supply relies is currently lacking.

The A_{max}–LN_{area} relationship is modified by different environmental factors and/or other nutrient limitations. Reduced water availability impacts this relationship mainly as a result of stomatal limitations for C fixation (e.g. Flexas & Medrano, 2002). Reich *et al.* (2009) also demonstrated that the initial slope of the relationship decreases with phosphorus deficiency associated with limitations in ribulose-1,5-bisphosphate regeneration. Peterson *et al.* (1999) showed that increased atmospheric CO_2 concentration increased the response of A_{max} to LN_{area}. Atkinson *et al.* (2010) determined that growing temperature altered the scaling of the relationship. According to these examples, significant scattering is expected when plotting A_{max} vs LN_{area} data compiled from independent studies. Under this scenario, a quantile regression approach would be useful to isolate the impact of LN_{area} on A_{max} in situations where other factors are not limiting. This analysis, performed at the 90th percentile for A_{max}, will allow the biological limit of the A_{max}–LN_{area} relationship to be determined for different cultivated and wild species. The relationship cannot change above that limit, but may be reduced when other factors are limiting. Therefore, using a quantile regression approach we will set the limits of this production-resource function (Cade & Noon, 2003; Archontoulis & Miguez, 2015). A quantile regression approach has been developed and successfully utilized to establish the maximum return of water invested in transpiration for crops (i.e. French & Schultz, 1984; Sadras & Angus, 2006). This study is the first to benchmark the upper limit for N use at the leaf level for different cultivated and wild species.

The ratio between A_{max} and LN_{area} defines the photosynthetic N-use efficiency as the amount of C fixed per unit of N invested in a leaf (PNUE; Poorter & Evans, 1998). As demonstrated by Dreccer *et al.* (2000), PNUE varies as a function of LN_{area}. Obtaining the PNUE from the A_{max}–LN_{area} relationship will also serve to benchmark the maximum PNUE for cultivated and wild species.

The objectives of this paper were: to determine the biological limit of the relationship between A_{max} and LN_{area} by benchmarking the parameters of the function defined in Sinclair & Horie (1989) for major cultivated and wild species; to contrast the relationship between PNUE and LN_{area} for major cultivated and wild species; and to determine the maximum PNUE and the LN_{area} at which it occurs for cultivated and wild species. We hypothesized that cultivated species will have increased photosynthetic N-use efficiency compared with wild species as possibly associated with artificial selection for resource-acquisition traits (Denison, 2009); this difference would be higher for annual cultivated species compared with cultivated perennials as the latter have a longer intergenerational period and therefore reduced cycles of selection.

Materials and Methods

Cultivated database compiled from published literature

To obtain data on cultivated species, a database was built from *ad hoc* species-specific bibliographic search. The search was oriented to papers on ecophysiological plant responses of different cultivated species from outdoor or glasshouse experiments at ambient CO_2 pressure. The papers reported the C exchange rate at light-saturated conditions (A_{max}) determined by infrared gas analyzer equipment (e.g. Li-Cor 6400 instrument, Lincoln, NE, or similar), and leaf N content on a leaf area basis (LN_{area}) in such a way as to reproduce these variables as $\mu mol\ CO_2\ m^{-2}\ s^{-1}$ and $g\ N\ m^{-2}$, respectively. Light-saturated conditions were reported in all cases, with light intensity ranging from 1200 to 2000 $\mu mol\ m^{-2}\ s^{-1}$ depending on the species. We excluded measures in hydroponic conditions or with increases in ambient CO_2 pressure. We obtained 48 papers that studied this relationship for 14 cultivated species, and we generally obtained three to 10 papers for each species (Supporting Information Table S1). The cultivated species were three C_3 winter cereal crops (*Triticum aestivum* (wheat), *Oryza sativa* (rice), and *Hordeum vulgare* (barley)), two summer C_4 cereal crops (*Zea mays* (maize) and *Sorghum bicolor* (sorghum)), five C_3 dicotyledonous annual crops (*Glycine max* (soybean), *Helianthus annuus* (sunflower), *Gossypium hirsutum* (cotton), *Brassica napus* (rapeseed), and *Solanum tuberosum* (potato)) and four cultivated trees (*Malus domestica* (apple), *Prunus dulcis* (almond), *Prunus persica* (peach), and *Citrus* × *paradise* (grapefruit)). For each paper we extracted the results from published scatter plots or data tables as paired observations of A_{max} and LN_{area}, totaling between 25 and 513 paired observations according to the species. A total of 2874 paired observations of A_{max} and LN_{area} for cultivated species were compiled from a period spanning from 1980 to 2012 (Tables S1, S2).

Wild database compiled from published literature

The search was oriented to papers on ecophysiological plant responses of different wild species with similar keywords as for the construction of the ‘cultivated’ database. Included papers reported outdoor or glasshouse studies that measured A_{max} and LN_{area} also in such a way to reproduce these variables as $\mu mol\ CO_2\ m^{-2}\ s^{-1}$ and $g\ N\ m^{-2}$, respectively. All papers included radiation measures and/or stated that A_{max} rate was measured under light-saturated conditions, which in most of cases ranged between 800 and 2000 $\mu mol\ m^{-2}\ s^{-1}$. We excluded measures in hydroponic conditions or with modifications in ambient CO_2 pressure. The life form (e.g. trees, grasses, dicotyledonous herbs, etc.) and C metabolism (i.e. C_3 or C_4) of the wild species were recorded to facilitate comparison against cultivated species characteristics. We obtained 35 papers that studied this relationship for wild species with measurements from the period 1981–2011 and across five continents (Tables S1, S2). In total we obtained 2326 paired observations of A_{max} and LN_{area} for wild species. The wild database included data from the GLOPNET database (Wright *et al.*, 2004).

For both cultivated and wild datasets, observations of $LN_{area} > 4\ g\ N\ m^{-2}$ associated with low C exchange rates were eliminated as possible outliers or species having specific adaptations for high investment in N with low return in terms of A_{max} (e.g. species producing alkaloids). These eliminated data represented < 0.1% of total revised data. All data used in the analysis were compiled into a unified database (Table S2).

Modeling the A_{max} vs LN_{area} relationship and statistical analysis

The relationship between A_{max} and LN_{area} was modeled following the logistic model proposed by Sinclair & Horie (1989):

$$A_{max} = \alpha \cdot \left[\frac{2}{\left(1 + e^{(-\beta(LN_{area} - \gamma))}\right)}\right] - 1 \qquad \text{Eqn 1}$$

where α is the asymptotic A_{max} at high LN_{area} values, β represents the curvature of the response between A_{max} and LN_{area}, and γ

indicates the LN_{area} value at which A_{max} is zero. This equation has the versatility to accommodate linear trends if needed through reduced β values. Data for the cultivated and wild species were analyzed by quantile regression for estimating parameters of the Sinclair & Horie (1989) model; conditional quantile functions at the 90th percentile from the QUANTREG package (Koenker, 2015) were used (R Core Team, 2013). After fitting models, goodness-of-fit tests such as the likelihood ratio test and a pseudo-R^2 were conducted (R_1; Koenker & Machado, 1999). The R_1 metric is a local measure of goodness of fit at a particular quantile. It compares the sum of weighted deviations from the model of interest with the same sum from a model in which only the intercept appears (null model). In addition, approximate confidence intervals (95%) for each parameter (i.e. α, β and γ) were built by bootstrapping (Koenker & Park, 1996; Koenker, 2005). The comparison among crops and wild species (see next section) was based on the punctual and interval estimates for each model parameter.

A leaf area-based analysis of the relationship between leaf photosynthesis and N was chosen as the alternative leaf mass-based approximation (i.e. g^{-1} leaf). There were two reasons for this decision. First, as solar radiation capture and C assimilation are intrinsically area-based processes, working on leaf area provides a suitable resource-harvesting framework to better understand N impacts on C capture (Field & Mooney, 1991), which is the major objective of our work. The mass-based analysis has been more appropriate to understand the economics of C and N allocation in species from contrasting habitats (Wright *et al.*, 2004). Second, the amount of area-based data is substantially higher than the amount of mass-based data. Therefore, focusing on mass-based data would have reduced the comprehensiveness of the database by reducing the total number of cases available for analysis.

Photosynthetic N-use efficiency was calculated as the quotient ratio between A_{max} and LN_{area} using the predicted values of the benchmarked model. PNUE was calculated only for the observed range of LN_{area} values. Maximum PNUE and LN_{area} at maximum PNUE were determined by first-degree derivation of the predicted relationship between PNUE and LN_{area}. Confidence intervals for the maximum PNUE across cultivated and wild species were built by propagating the uncertainty of estimates from the original quantile regression on A_{max} and LN_{area}, and assuming a lack of error in the punctual estimation of the LN_{area} for maximum PNUE. To conduct this analysis we used the package PROPAGATE (Spiess, 2014) from the R environment, and the comparison among cultivated and wild species was based on the punctual and interval estimates for the maximum PNUE.

Comparison of cultivated and wild species

Individual cultivated species were compared against the best equivalent wild species functional groups. For instance, cultivated C_3 winter cereals (i.e. wheat, rice, and barley) were compared against wild C_3 graminoids. The C_4 summer cereal crops (i.e. maize and sorghum) were compared against C_4 wild graminoids. The C_3 dicotyledonous annual crops (i.e. soybean, sunflower, rapeseed, cotton, and potato) were compared against the wild C_3 dicotyledonous herbaceous plants. The perennial fruit/nut cultivated trees were compared against C_3 woody plants. The rationale behind not grouping the cultivated species is that it is highly relevant analyzing these 14 species individually, as they represent most of the primary production worldwide. By grouping the wild species, we sought to determine the limits of PNUE for wild species as a reference group, regardless of the individual species. For each cultivated species and wild functional group, we built the respective scatter plot relating A_{max} and LN_{area}.

Results

Cultivated C_3 winter cereals vs wild C_3 graminoids

Sinclair & Horie (1989)'s model fitted for the C_3 cultivated cereals and C_3 wild graminoids was significant, with R_1 ranging from 0.28 to 0.64 (Table 1). Wheat and rice had a lower A_{max} at maximum LN_{area} (α in Eqn 1) compared to the wild C_3 graminoids, while barley was not different from wild species (Table 2; Fig. 1a–c). The curvature of the relation between A_{max} and LN_{area} (β in Eqn 1) was higher for wheat and rice than for the wild C_3 graminoids; there was no difference in this parameter between barley and the wild counterparts (Table 2). The minimum LN_{area} for $A_{max} > 0$ (γ parameter, Eqn 1) was significantly higher for barley when compared to C_3 wild graminoids (Table 2).

Wheat and rice had higher maximum PNUE than the wild species, attained at relatively low LN_{area} (~1 g N m^{-2}) (Table 2;

Table 1 Summary of goodness-of-fit tests for different wild plant functional types and related cultivated species based on the log-likelihood ratio and respective chi-squared tests, and pseudo-R^2 measures (R_1)* for the Sinclair & Horie (1989) model at the 90th percentile

Wild groups and related crops	Log-likelihood null model	Log-likelihood Sinclair	$\chi^2_{(2)}$	*P*-value	R_1
C_3 graminoids	−1390.5	−1207.08	365.4	< 0.0001	0.43
Wheat	−829.7	−682.7	294.1	< 0.0001	0.50
Rice	−1084.3	−976.5	215.5	< 0.0001	0.28
Barley	−618.6	−456.3	324.6	< 0.0001	0.64
C_4 graminoids	−271.65	−269.48	4.33	0.1146	0.03
Maize	−1136.7	−1079.5	114.4	< 0.0001	0.20
Sorghum	−539.4	−462.8	153.1	< 0.0001	0.43
C_3 dicot herbs	−2347.3	−2054.3	586.1	< 0.0001	0.41
Soybean	−1420.2	−1259.5	321.2	< 0.0001	0.36
Sunflower	−1292.3	−1154.2	276.1	< 0.0001	0.33
Cotton	−1949.5	−1913.1	72.7	< 0.0001	0.07
Rapeseed	−563.5	−528.8	69.5	< 0.0001	0.22
Potato	−275.3	−216.9	116.8	< 0.0001	0.49
C_3 trees	−4061.2	−3648	826.4	< 0.0001	0.31
Apple	−73.6	−39.8	67.6	< 0.0001	0.74
Almond	−272.3	−245.5	56.3	< 0.0001	0.28
Peaches	−254.9	−218.9	71.8	< 0.0001	0.36
Grapefruit	−181.1	−163.9	34.1	< 0.0001	0.22

*R_1 is described as a local measure of goodness of fit at the particular quantile by comparing the sum of weighted deviations for the model of interest with the same sum from a model in which only the intercept appears.

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Table 2 Parameters relating light-saturated photosynthesis rate (A_{max}) and leaf nitrogen content (LN_{area}) for C_3 monocots

Functional group and related crops	Fitted parameters (95% CI) α	β	γ	Max. PNUE (95% CI)	LN_{area} at max PNUE
C_3 wild graminoids	61.3 (43.7–78.8)	0.68 (0.41–0.95)	0.15 (0.07–0.22)	17.6 (14.2–18.3)	1.38
Wheat	36.3 (32.8–39.8)	1.61 (1.19–2.02)	0.23 (0.11–0.34)	20.1 (18.1–21.2)	1.01
Rice	33.2 (28.3–38.1)	2.01 (1.06–2.94)	0.22 (0.02–0.42)	21.74 (17.6–22.6)	0.90
Barley	59.1 (44.8–73.4)	0.96 (0.59–1.32)	0.31 (0.25–0.38)	20.2 (16.9–20.7)	1.56

Summary of quantile regression analysis (90th percentile) between A_{max} (μmol CO_2 m^{-2} s^{-1}) and LN_{area} (g N m^{-2}) for C_3 wild graminoids and related crops (wheat, rice and barley). Numbers indicate the punctual estimates for the parameters of the Sinclair & Horie (1989) model model (α, maximum A_{max}; β, the curvature of the relationship; and γ, minimum N leaf area for photosynthesis), as well the maximum photosynthetic nitrogen-use efficiency (PNUE; μmol CO_2 g^{-1} N s^{-1}), and the punctual LN_{area} at maximum PNUE. Values between parentheses are the confidence intervals of the estimates.

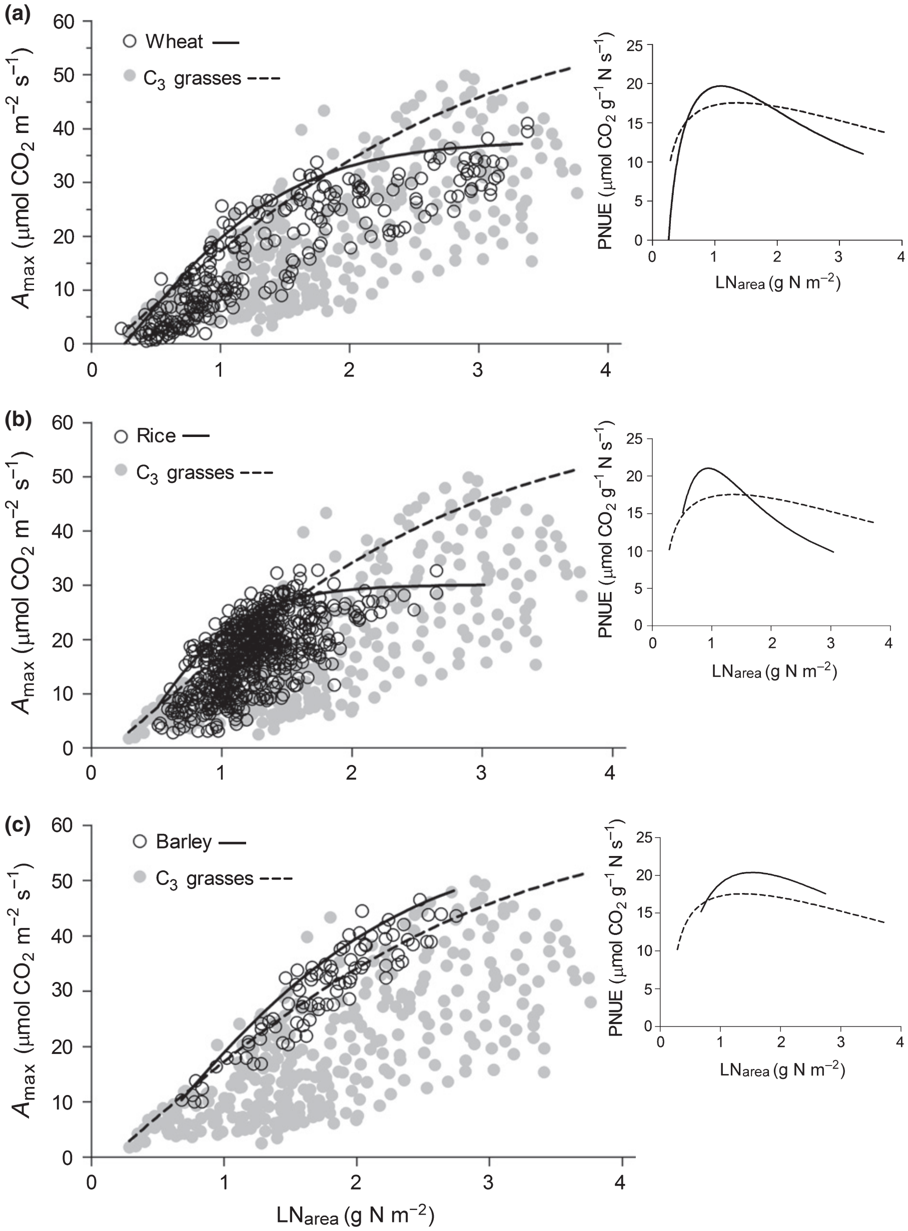

Fig. 1 Quantile regression models for the relationship between the light-saturated photosynthesis rate (A_{max}; μmol CO_2 m^{-2} s^{-1}) and the leaf nitrogen content (LN_{area}; g N m^{-2}) for wild C_3 graminoids (dashed line and gray markers) and related crop species (solid line and white markers): (a) wheat; (b) rice; (c) barley. Insets: the predicted photosynthetic nitrogen-use efficiency (PNUE; μmol CO_2 g^{-1} N s^{-1}) along the same leaf nitrogen content gradient according to the fitted model.

Fig. 1a,b insets); the barley maximum PNUE was attained at a higher LN_{area} (1.56 g N m^{-2}) compared with the other cultivated species, and was not significantly different from the wild species. Wheat and rice were more efficient than wild C_3 graminoids at LN_{area} < 1.5 g N m^{-2} (Table 2; Fig. 1 insets).

Cultivated C_4 cereals vs C_4 wild graminoids

Sinclair & Horie's model fitted for C_4 cultivated species was significant, with $R_1 = 0.2$ for maize and $R_1 = 0.43$ for sorghum; however, the model fitted for the wild C_4 graminoid species was not significantly different from the null model represented only by the intercept ($\alpha = 42.3$) (Table 1). Maize α was significantly higher compared to the C_4 wild graminoids (Table 3). Sorghum had a significantly higher α than maize and the wild C_4 counterparts (Table 3; Fig. 2b). Owing to the high uncertainty in the estimation of β for the C_4 wild species, there were no significant differences for this parameter between cultivated and wild C_4 grasses. The γ parameter for maize and sorghum was not different from zero, and was not different from wild C_4 estimates (Table 3).

Maize and sorghum maximum PNUE values were approximately half that of wild C_4 species (Table 3). These maximums were also achieved near to the origin (0.28–0.34 g N m^{-2}, Table 3; Fig. 2 insets). As wild and cultivated C_4 species present γ estimates < 0, the relationship between PNUE and LN_{area} showed a decreasing trend from their maximum (Fig. 2 insets). Wild C_4 PNUE was higher than that for the C_4 crops below *c.* 1 g N m^{-2} leaf; above this value, differences between crops and wild C_4 graminoids were not evident (Fig. 2 insets).

Cultivated C_3 dicotyledonous annuals vs wild C_3 dicotyledonous herbaceous

Sinclair & Horie's models fitted for cultivated C_3 dicotyledonous species and C_3 wild herbs were significant, with R_1 in the range 0.07–0.49 (Table 1). The α parameter for soybean, sunflower, and rapeseed was not different from that for wild C_3 herbs (Table 4; Fig. 3a,b,d); cotton and potato, on the other hand, had a lower α than wild C_3 herbs (Table 4; Fig. 3c,e). A higher β was observed for sunflower, cotton and potato than for the wild C_3 herbs (Table 4); soybean and rapeseed were not significantly different from their wild counterpart. For all the C_3 dicotyledonous crops, except potato, the minimum LN_{area} for photosynthesis (γ) was higher than zero (0.238–0.615 g N m^{-2}) and significantly higher than that for wild C_3 herbs (Table 4; Fig. 3). However, the γ estimate for potato was not different from zero and not different from that for wild C_3 herbs.

The maximum PNUE values for sunflower, cotton, and rapeseed were not different from those for the wild species (Table 4; Fig. 3b–d insets). Soybean and potato have the lowest maximum PNUE, with a significant reduction of 39–47% compared with wild species (Table 4; Fig. 3a,e insets). The difference in the PNUE–LN_{area} relationship between cultivated and wild species was a result of the remarkable difference in the γ parameter. The maximum PNUE occurred at a relatively low LN_{area} (0.23 g N m^{-2}) in wild species, while the maximum PNUE for the cultivated species was observed at intermediate values (0.65–1.72 g N m^{-2}) (Table 4; Fig. 3 insets).

Cultivated fruit/nut trees vs C_3 woody plants

All Sinclair & Horie's models fitted for cultivated C_3 trees and wild woody C_3 species were significant, with R_1 ranging from 0.22 to 0.74 (Table 1). Grapefruit was the cultivated C_3 tree with the lowest α compared with both the wild trees and the remaining of the cultivated ones (Table 5; Fig. 4d). Apple, almond, and peach were not different from the C_3 wild trees for the α parameter (Table 5; Fig. 4a–c). For all C_3 crop trees except almond, the β parameter was not different compared with the wild trees; almond, on the other hand, had a significantly higher β than did the wild trees (Table 5). For all the cultivated C_3 trees, γ was significantly higher compared with the C_3 wild trees (Table 5).

Owing to the negative γ estimate of C_3 wild trees, the PNUE for this group was highest at infinitesimally low LN_{area} (Fig. 4). Wild trees had a maximum PNUE of 31.6 μmol CO_2 g^{-1} N s^{-1}, attained at 0.11 g N m^{-2} (Table 5). The maximum PNUE of cultivated C_3 trees was, on average, 8.6 μmol CO_2 g^{-1} N s^{-1}, attained at an average LN_{area} of 1.7 g N m^{-2}. For all cultivated trees, the values of maximum PNUE and LN_{area} at highest

Table 3 Parameters relating light-saturated photosynthesis rate (A_{max}) and leaf nitrogen content (LN_{area}) for C_4 monocots

Functional group and related crops	Fitted parameters (CI 95%) α	β	γ	Max. PNUE (CI 95%)	LN_{area} at max. PNUE
C_4 wild graminoids	42.3 (38.9–45.8)	6.25 (−23.1–35.6)	−0.05 (−4.7–4.9)	206.2 (188.8–222.3)	0.21
Maize	52.1 (45.4–58.9)	2.40 (0.81–4)	−0.09 (−0.43–0.25)	74.7 (68.2–81.9)	0.28
Sorghum	59.4 (53.4–64.9)	1.69 (0.79–2.58)	−0.17 (−0.6–0.26)	71.0 (49.8–86)	0.34

Summary of quantile regression analysis (90th percentile) between A_{max} (μmol CO_2 m^{-2} s^{-1}) and LN_{area} (g N m^{-2}) for C_4 wild graminoids and related crops (maize and sorghum). Numbers indicate the punctual estimates for the parameters of the Sinclair & Horie (1989) model (α, maximum A_{max}; β, the curvature of the relationship; and γ, minimum LN_{area} for photosynthesis), as well the maximum photosynthetic nitrogen-use efficiency (PNUE; μmol CO_2 g^{-1} N s^{-1}), and the punctual LN_{area} at maximum PNUE. Values between parentheses are the confidence intervals of the estimates.

PNUE were lower and higher, respectively, than those for the wild trees. However, both groups explored a different range of LN_{area} (Fig. 4). The comparison of the relationship between PNUE and LN_{area} in the *x*-axis range shared by the cultivated and wild trees showed a near-identical response for these groups in terms of PNUE performance across varying LN_{area} (Fig. 4).

Discussion

The development of modern agriculture moved plants from wild environments to cultivated lands with higher resource abundance and lower pest/disease pressure (Evans, 1993). Plant strategy theory predicts trajectories during crop evolution shifting from a

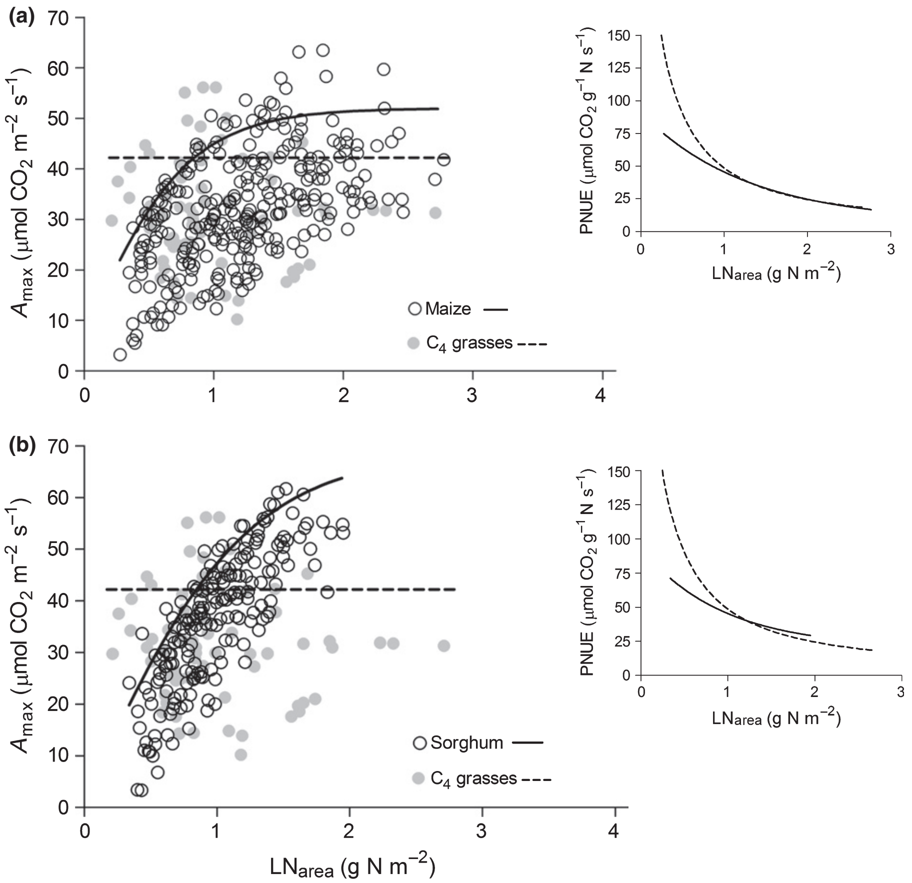

Fig. 2 Quantile regression models for the relationship between the light-saturated photosynthesis rate (A_{max}; μmol CO_2 m^{-2} s^{-1}) and the leaf nitrogen content (LN_{area}; g N m^{-2}) for wild C_4 graminoids (dashed line and gray markers) and related crop species (solid line and white markers): (a) maize; (b) sorghum. Insets: the predicted photosynthetic nitrogen-use efficiency (PNUE; μmol CO_2 g^{-1} N s^{-1}) along the same leaf nitrogen content gradient according to the fitted model.

Table 4 Parameters relating light-saturated photosynthesis rate (A_{max}) and leaf nitrogen content (LN_{area}) for C_3 dicot herbs

Functional group and related crops	Fitted parameters (95% CI) α	β	γ	Max. PNUE (95% CI)	LN_{area} at max. PNUE
C_3 wild herbs	51.3 (45.8–56.8)	0.87 (0.65–1.08)	−0.02 (−0.11–0.08)	23.9 (15.4–28.1)	0.23
Soybean	55.3 (41.8–68.7)	0.65 (0.39–0.91)	0.24 (0.13–0.35)	14.4 (10.8–14.9)	1.72
Sunflower	46.0 (42.4–49.6)	1.33 (1.06–1.6)	0.28 (0.12–0.43)	21.3 (19.2–22.2)	1.15
Cotton	40.0 (37.9–42.2)	2.27 (1.23–3.3)	0.62 (0.31–0.93)	20.4 (15.4–22.5)	1.46
Rapeseed	46.9 (35.6–58.1)	1.92 (0.73–3.12)	0.38 (0.23–0.53)	25.7 (12.7–28.9)	1.19
Potato	20.7 (17.9–23.4)	1.44 (0.95–1.93)	0.07 (−0.1–0.24)	12.6 (10.3–13.9)	0.65

Summary of quantile regression analysis (90th percentile) between A_{max} (μmol CO_2 m^{-2} s^{-1}) and LN_{area} (g N m^{-2}) for C_3 wild dicotyledonous herbs and related crops (soybean, sunflower, cotton, rapeseed, and potato). Numbers indicate the punctual estimates for the parameters of the Sinclair & Horie (1989) model (α, maximum A_{max}; β, the curvature of the relationship; and γ, minimum LN_{area} for photosynthesis), as well the maximum photosynthetic nitrogen-use efficiency (PNUE; μmol CO_2 g^{-1} N s^{-1}), and the punctual LN_{area} at maximum PNUE. Values between parentheses are the confidence intervals of the estimates.

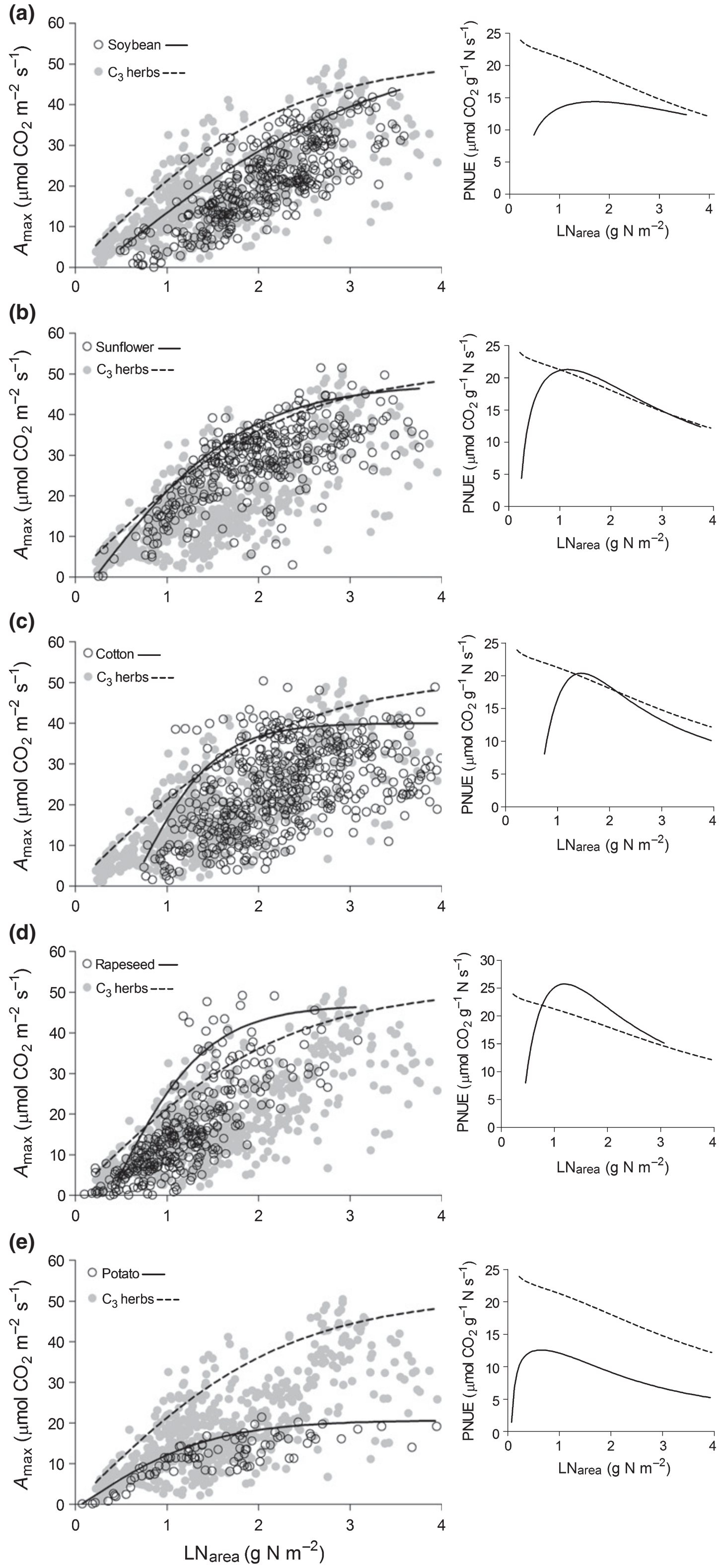

Fig. 3 Quantile regression models for the relationship between the light-saturated photosynthesis rate (A_{max}; μmol CO_2 m^{-2} s^{-1}) and the leaf nitrogen content (LN_{area}; g N m^{-2}) for wild C_3 dicotyledonous herbs (dashed line and gray markers) and related crop species (solid line and white markers): (a) soybean; (b) sunflower; (c) cotton; (d) rapeseed; (e) potato. Insets: the predicted photosynthetic nitrogen-use efficiency (PNUE; μmol CO_2 g^{-1} N s^{-1}) along the same leaf nitrogen content gradient according to the fitted model.

resource-conservation to a resource-acquisition suite of traits (Denison, 2009). In this sense, we expected to see a high proportion of cultivated species surpassing the wild species for the A_{max}–LN_{area} relationship. However, our findings support the concept that the cultivated species have not surpassed the biological limit of N use for plant photosynthesis observed for wild species. It can be speculated that potential differences between cultivated and wild species are attributed to crop domestication, artificial selection, and/or cultivation environment. Testing some of these hypotheses requires a more targeted comparison between

Table 5 Parameters relating light-saturated photosynthesis rate (A_{max}) and leaf nitrogen content (LN_{area})for C_3 dicot trees

Functional group and related crops	Fitted parameters (CI 95%) α	β	γ	Max. PNUE (95% CI)	LN_{area} at max. PNUE
C_3 wild trees	30.5 (19.2–41.8)	0.54 (0.26–0.82)	−0.27 (−0.42 to −0.13)	31.6 (17.8–36.1)	0.11
Apple	23.2 (19.3–27.1)	0.84 (0.45–1.23)	0.23 (−0.10–0.57)	7.5 (6.3–7.9)	1.46
Almond	22.9 (19.9–25.8)	4.13 (1.55–6.71)	1.63 (1.53–1.74)	8.8 (5.5–9.2)	2.35
Peaches	23.7 (18.1–29.3)	1.22 (0.46–1.97)	0.39 (0.08–0.71)	9.3 (6.5–9.7)	1.52
Grapefruit	16.6 (14.8–18.3)	2.02 (0.16–3.88)	0.51 (−0.08–1.11)	8.6 (2.1–9.4)	1.46

Summary of quantile regression analysis (90th percentile) between A_{max} (μmol CO_2 m^{-2} s^{-1}) and LN_{area} (g N m^{-2}) for C_3 wild trees and related cultivated species (apple, almond, peaches, and grapefruit). Numbers indicate the punctual estimates for the parameters of the Sinclair & Horie (1989) model (α, maximum A_{max}; β, the curvature of the relationship; and γ, minimum LN_{area} for photosynthesis), as well the maximum photosynthetic nitrogen-use efficiency (PNUE; μmol CO_2 g^{-1} N s^{-1}), and the punctual LN_{area} at maximum PNUE. Values between parentheses are the confidence interval of the estimates.

cultivated species and their specific ancestors. For example, in a comprehensive screening of cultivated vs wild ancestors, Milla *et al.* (2015) showed that wild progenitors of modern crops were already high resource-acquisition and utilization strategists. Preece *et al.* (2015) also showed that wild progenitors did not have any advantage in terms of resource acquisition compared with wild plants that were not selected for domestication. Similarly, higher PNUE has been observed in undomesticated *Glycine soja* compared with the domesticated *Glycine max* cultivars (Rotundo & Borrás, 2016). Domestication seems to have involved changes in other specific traits associated with seed shedding, biomass partitioning, and sensitivity to photoperiod (Ulukan, 2009).

Our evaluation provides parameters for the potential relationship between A_{max} and LN_{area} for major cultivated species and wild plant functional types, representing two major improvements on previous efforts to compile leaf photosynthesis data. First, previous comparisons focused on smaller sets of cultivated species. Evans (1989) compared only wheat and rice against a set of wild species. Wullschleger (1993) characterized di- and monocots crops as individual groups. Kattge *et al.* (2009) compared wild functional groups and C_3 cultivated species as a group. Our study is unique in that it reports a comparison of 14 major cultivated species against equivalent wild functional groups. Second, compiling a diverse set of data and performing a unique analysis are always challenging as data were, most probably, obtained under different environmental conditions. The frontier analysis followed here, set at the 90th percentile of the A_{max}–LN_{area} relationship, provides the opportunity to eliminate the influence of any additional factor that is reducing the ability of a leaf to fix C (e.g. climatic conditions, nutrients other than N, etc.). The quantile regression approach, entirely novel to this area, allowed us to benchmark the potential ability to use N for C fixation in major cultivated species for world food and feeding and wild plants from natural ecosystems.

The difference between cultivated and wild species for the parameters of the A_{max}–LN_{area} relationship depended on each particular parameter. First, in terms of A_{max} at saturating LN_{area} (α), only maize and sorghum surpassed the wild species; it was lower in wheat, rice, cotton, potato, and grapefruit, and not different in the remaining eight cultivated species. Operating at high LN_{area} (and high A_{max}) would not be evolutionary stable as this is frequently associated with reduced leaf area, reduced light interception, and reduced fitness (yield) (Sinclair & Horie, 1989). Second, the curvature of the relationship (β) was higher in five cultivated species (wheat, rice, sunflower, cotton, potato, and almond), compared with the wild counterparts. An increased curvature is generally associated with increased A_{max} at intermediate LN_{area} values. Selecting for cultivated populations having increased A_{max} at intermediate values of LN_{area} would not have costs in terms of reduced LAI that may limit light interception and it could be a trait selectable for increased yields. Finally, the minimum amount of LN_{area} for photosynthesis was higher compared with wild species in all but five cultivated species that did not differ from their wild counterparts (rice, wheat, maize, sorghum, and potato). The higher γ commonly found in these cultivated species may be associated with relaxed herbivory pressure which allows for more N-expensive leaves that are protected via chemical applications (Coley *et al.*, 1985). An alternative explanation is that the wild database also incorporated species from N-limited environments with inherent low LN_{area} (Chapin, 1980).

With few exceptions, cultivated species PNUE values were inferior to, or not different from, those of the wild species. Wheat and rice had a steeper initial slope than did the wild species, determining a high PNUE at relatively low LN_{area} (< 2 g N m^{-2}). In general, LN_{area} changes from early stages to maturity range from 2.0 to 0.9 g N m^{-2} and from 1.7 to 0.8 g N m^{-2} in wheat and rice, respectively (Ohsumi *et al.*, 2007; Bertheloot *et al.*, 2008). These ranges match well those LN_{area} values where PNUE tends to be highest for those crops. The high A_{max} observed in both crops may be caused by greater N allocation to Rubisco (Makino *et al.*, 1992). Whether the higher PNUE observed in wheat and rice than in the wild C_3 grasses is also going to be valid

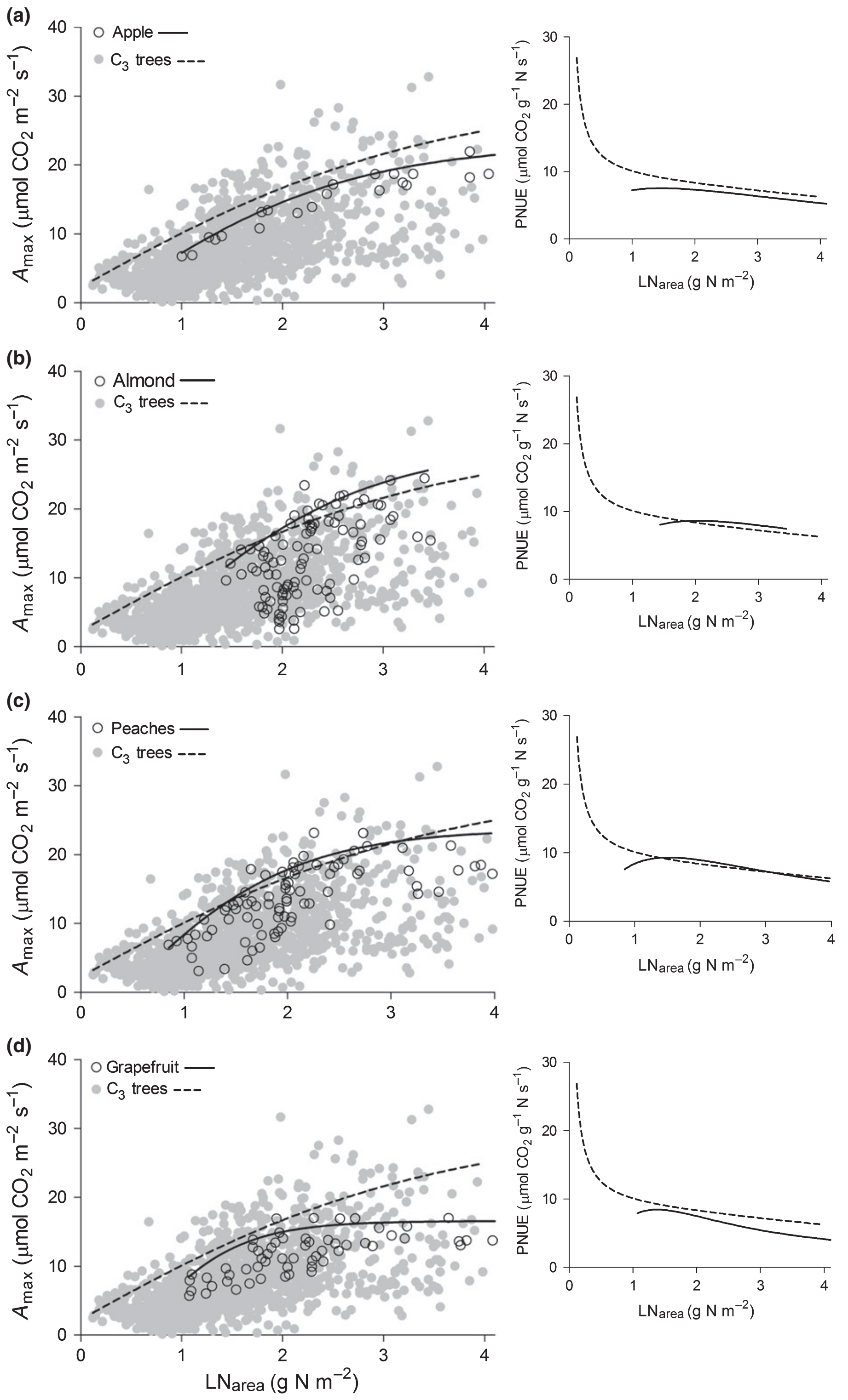

Fig. 4 Quantile regression models for the relationship between the light-saturated photosynthesis rate (A_{max}; μmol CO_2 m^{-2} s^{-1}) and the leaf nitrogen content (LN_{area}; g N m^{-2}) for wild C_3 trees (dashed line and gray markers) and related cultivated species (solid line and white markers): (a) apple; (b) almond; (c) peaches; (d) grapefruit. Insets: the predicted photosynthetic nitrogen-use efficiency (PNUE; μmol CO_2 g^{-1} N s^{-1}) along the same leaf nitrogen content gradient according to the fitted model.

in a global change scenario remains to be determined. There is evidence that increased CO_2 concentration has a positive effect on A_{max} in C_3 species (Ainsworth & Long, 2005; Tubiello *et al.*, 2007). The relative responses of A_{max} to increased CO_2 were similar in C_3 crops and C_3 grasses (Ainsworth & Long, 2005; Tubiello *et al.*, 2007). Therefore, we can speculate that increases in PNUE associated with increased A_{max} would be similar for these groups of species, maintaining the differences currently observed. However, this positive effect of CO_2 on A_{max} could be cancelled to some degree by increases in temperature (Lobell & Gourdji, 2012).

Maize and sorghum had lower PNUE values, < 1 g N m^{-2}, compared with C_4 wild grasses. Muchow & Sinclair (1994) showed that, in general, maize and sorghum operate at different

LN_{area} (1.8 and 1.3 g N m^{-2} in maize and sorghum, respectively). In both cases, these LN_{area} values are within the range of those determining similar PNUE values to C_4 wild grasses.

The C_3 dicotyledonous annual crops had similar PNUE values to the C_3 wild herbs, at least from values of *c.* 1 g N m^{-2} upwards. The exceptions were soybean and potato, having lower PNUE than the wild C_3 herbs in a wide range of LN_{area}. Soybean leaves are N storage organs synthesizing vegetative storage protein (Staswick, 1994). This protein can account for almost 50% of total soluble protein in the leaves; the presence of these N-rich proteins may help to explain the low PNUE observed for this crop. Potato, on the other hand, has been reported as a species having inherently low leaf PNUE than other crops (Vos & van der Putten, 1998). The low PNUE can also explain the low NUE observed at crop level (Ospina *et al.*, 2014).

The C_3 cultivated trees were not different in their PNUE response to LN_{area} from the C_3 wild woody species. Because of the long times required for commercial tree breeding, it was expected that there would not be meaningful differences from their wild counterparts. One interesting aspect of this comparison is that the LN_{area} of crop trees was never < 1 g N m^{-2}, as it was for the wild trees. One hypothesis we propose to explain this finding is that farming ensured more N availability to crop trees, whereas wild trees grow and evolve in climax communities characterized by low availability of soil nutrients, especially those from tropical or subtropical rainforests (Thompson *et al.*, 1992; Reich *et al.*, 1994). In addition, it was reported that the leaf N concentration changed among tree species according to the optimal functioning for C fixation related to the shade tolerance syndrome (Niinemets & Tenhunen, 1997); the wild tree database included some understory species that had low LN_{area} associated with this syndrome. Another hypothesis to explain lower LN_{area} in wild vs cultivated trees has to do with seasonal variations in temperature and soil water content (Muller *et al.*, 2011; Sugiura & Tateno, 2011); for example, wild tree measurements in the dry season in tropical regions may have reduced LN_{area}. Leaf N also depends on the amount of radiation in a vertical gradient of light incident across a dense canopy (Hikosaka, 2016); wild trees may be adapted to reduced amounts of radiation (and hence invest lower LN_{area}) as they evolved in dense canopies. In the case of cultivated trees, these species are grown in near isolation, without understory competition from herbaceous communities, and with supplemental fertilization (Tagliavini *et al.*, 1995; Zarate-Valdez *et al.*, 2015). Also, chemical protection in commercial orchards prevented pests and diseases that are more prone to occur in leaves with greater N concentrations (Coley *et al.*, 1985).

Findings from our work have implications in both the agricultural and ecological domains. In the agricultural domain, securing food demand requires understanding of ecophysiological constraints to increase C fixation of cultivated species (FAO, 2009; Tilman *et al.*, 2011). Our results show almost no advantages for cultivated species to fix more C in the physiological frontier along a wide range of N leaf contents when compared with wild species. There is evidence, however, that photosynthesis is not fully optimized, suggesting that there are possibilities to increase crop yields by improving this process (e.g. Murchie *et al.*, 2009). In the near future, it is likely that novel biotechnologies will explore alternative ways to increase A_{max} and PNUE at the cell level, including synthetic C fixation pathways (Bar-Even *et al.*, 2010; Raines, 2011; McGrath & Long, 2014) able to move up this physiological frontier. In the ecological domain, C fixation and sequestration among wild species in natural terrestrial ecosystems have a prominent role to play in attenuating the consequences of current climate change (Lai, 2004; Davidson & Janssens, 2006).

Acknowledgements

J.L.R. and P.A.C. are profoundly grateful to their teacher, Martín Roberto Aguiar, for introducing them to and guiding them through the first steps of the fascinating world of ecological science and for sharing the happiness of delving into the mysteries of the Patagonian rangelands. This manuscript is only a small piece of our homage to him, and our everlasting acknowledgment of his commitment during more than 30 yr of teaching. We also thank to Amy Austin for her helpful comments on an earlier version of this manuscript. J.L.R. and P.A.C. are members of CONICET, the National Research Council for Argentina.

Author contributions

J.L.R. and P.A.C. designed the research, compiled the database, analyzed the data, and wrote the paper.

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Additional Supporting Information may be found online in the Supporting Information tab for this article:

Table S1 Bibliographic references included in the meta-analysis

Table S2 Dataset included in the meta-analysis

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