CSIRO PUBLISHING
www.publish.csiro.au/journals/trj *The Rangeland Journal*, 2005, **27**, 135–142

Growth characteristics associated with biomass production in three varieties of *Trichloris crinita* (Poaceae), a forage grass native to the arid regions of Argentina

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Abstract. *Trichloris crinita* (Lag.) Parodi is an important perennial native grass widespread in the range areas of the arid and semi-arid phytogeographical region of Monte, Argentina. Previous studies have shown great variability in forage biomass production per plant among different varieties of this species. The aim of this work was to assess which morphological and physiological traits are associated with differential productivity of *T. crinita* varieties. Three varieties: Pichi, of high productivity, Arroyito, of medium productivity, and Encon, of low productivity were tested in a field experiment. Dry matter (DM) produced by different organs, assimilates partitioning, and leaf area per plant were measured on three different dates for each variety, during an annual growth cycle, under watered conditions. Relative growth rate (RGR), net assimilation rate (NAR), leaf area ratio (LAR), specific leaf area (SLA), leaf weight ratio (LWR) and leaf area development rate (LADR) were calculated at 72, 128 and 172 days after transplanting. Significant differences among varieties were found for DM production of blades, sheaths + culms, panicles, roots and shoot/root ratio. Pichi and Arroyito produced more total plant biomass than Encon and this was associated with higher dry matter accumulation in aboveground organs and larger leaf area. LADR, LAR and one of its components SLA were the parameters that best explained differences in biomass production. DM partitioning to roots (considered as the percentage of total DM) was very high in Encon, the least productive variety. Differences in productivity seem to be directly associated with the mean annual rainfall and inversely associated with the mean annual temperature of the environment where plants were collected. Thus, the growth characteristics of each variety reflect differential adaptation to their areas of origin.

Additional keywords: intraspecific variability, partitioning, specific leaf area.

Introduction

Native grasses are important for range grazing in arid and semi-arid regions, as they are the main forage resources in these ecosystems. Species from arid and semiarid regions have special features that may confer advantages for higher productivity under stress conditions (Turner 1979). Varieties or ecotypes from the same grass species frequently show variation in morphological and physiological traits that may account for their differential performances under such environments. Therefore, in order to perform an efficient plant breeding selection, it is important to know which traits account for differences in productivity. In particular, it is important to focus on those processes directly involved in yield (Hall 1980; Boyer 1982).

Trichloris crinita (synonymous = *Chloris crinita*), which is a C_4 species, is one of the most important perennial native grasses in the west arid region of Argentina known as 'Monte' (Cavagnaro 1988), mainly due to its forage quality and its wide area of distribution (Waistein and González 1969; Roig 1971). Previous work comparing 18 varieties of this species in three different environments within the Monte Region showed great differences in forage production (Cavagnaro *et al*. 1989; Passera *et al*. 1997). Here, annual dry matter production per plant varied 10-fold between the least (20 g) and most (205 g) productive varieties.

In some species, total dry matter production is not always associated with photosynthetic rate per unit of leaf area. Instead, it may depend on many factors including life-history characteristics, canopy structure, respiration rates, translocation and partitioning of assimilates and environmental conditions (Nasyrov 1978; Lambers 1987; Poorter *et al*. 1991; Poorter and Pothmann 1992; Reich 1998). Newly-developed varieties of most crop species may have the same total plant biomass as old ones but differ in the

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proportion of biomass allocated to each organ. Gifford and Evans (1981) and Gifford *et al*. (1984) demonstrated that increased yield in modern varieties of cereals, soybean, etc., is not due to higher photosynthetic rates or higher total biomass, but rather, to a larger assimilate partitioning to sink organs that are of interest for human consumption: i.e. they had a larger harvest index. Based on those papers, our first hypothesis was that the higher productivity shown by some varieties of *T. crinita* was due to a larger DM partitioning to shoots than to roots.

In addition to differences in DM partitioning, we demonstrated that those varieties of *T. crinita* with higher productivity showed a higher total dry matter production per plant (Greco and Cavagnaro 2003), which was not found by Gifford and Evans (1981) and Gifford *et al*. (1984) with some crops species. Thus, we also postulate that their higher biomass production could be due to an increased rate of leaf area development.

Plants species may differ greatly in their inherent growth rate, even when they are grown under optimal conditions. Genetic variations responsible for differences in growth rate arise from evolutionary selection under diverse environments. In general, species from rich environments present higher growth rate than those from poor sites (Grime and Hunt 1975; Lambers 1987; Poorter and Remkes 1990; Hunt and Cornelissen 1997; Reich 1998; Poorter and Nagel 2000). A higher dry matter production has been associated with certain morphological and physiological leaf characteristics such as net assimilation rate (NAR, increase in plant DM per unit of leaf area and unit of time), leaf area ratio (LAR, ratio total leaf area/total plant weight), specific leaf area (SLA, ratio leaf area/leaf weight), and leaf weight ratio (LWR, fraction of plant biomass allocated to leaves) (Lambers 1987; Poorter and Remkes 1990; Garnier 1992; Hunt and Cornelissen 1997; Poorter and Evans 1998; Poorter and Nagel 2000; Evans and Poorter 2001).

According to Schulze (1983), differences in partitioning among different life forms could have provided adaptive advantages to species under certain environmental conditions. This work deals with only one life form, perennial grasses, but with three varieties differing in productivity. We also are interested in determining whether the differences in productivity are associated with differences in temperature and rainfall in their native environments.

The objective of this work was to investigate which traits are associated with higher DM production in three varieties of *Trichloris crinita* contrasting in their biomass production. The relationships among these traits and the environment of each variety are also discussed.

Materials and methods

The phytogeographical province of 'Monte' is an extended north–south area located along the eastern base of the Andes Mountains in Argentina (Fig. 1). It is a shrubland dominated by species of the genus *Larrea* interspersed with grasses and other herbaceous species (Morello 1958; Cabrera 1976) as well as a few tree species, mostly of *Prosopis* genus. The latter is mainly found in areas where groundwater is present. A comprehensive description of the structure and function of the flora and fauna in this warm desert has been compiled by Orians and Solbrig (1977). Under natural conditions *Trichloris crinita* (Lag.) Parodi behaves as a typical aestival species growing whenever soil water is available and temperature is above 10°C (Seligman *et al*. 1992).

The trial was conducted in the experimental field of IADIZA (Instituto Argentino de Investigación de Zonas Aridas), Mendoza, Argentina (32°53′S; 68°51′W; 827 m altitude) (Fig. 1). Mean annual rainfall is 245 mm, occurring mainly in summer. Mean temperature is 8°C in July, and 24°C in January. South-easterly winds are predominant at a mean velocity of 9.5 km/h.

Varieties used in this trial originated from seeds obtained from a single plant and propagated during five generations. We called these plant materials 'varieties' rather than 'ecotypes' since they may not represent the whole sampled population, but only a fraction of it (King and Standfield 1997). The mother plant was chosen because it was the most frequently observed phenotype of a certain population. These varieties did not segregate after 5 generations under open pollination conditions so we suppose they probably are autogamous or apomictic. Populations were collected in different environments of the Monte (Fig. 1).

Three varieties of different productivities were assayed: (1) Pichi, of high productivity, (2) Arroyito, of medium productivity, and (3) Encon, of low productivity; from now on referred to as Pichi, Arroyito and Encon, respectively. The mean aboveground plant biomass evaluated in a 3-year trial performed in 3 sites of the Monte, was 205, 90 and 40 g DM/plant.year for Pichi, Arroyito and Encon, respectively (Cavagnaro *et al*. 1989). The name 'Pichi' derives from Pichi Ciego, Mendoza (33°50′S, 68°12′W); 'Arroyito' from Arroyito, Mendoza (32°50′S, 67°27′W) and 'Encon' from El Encon, San Juan, (32°09′S, 67°59′W) (Fig. 1). The most important climatic variables and soil characteristics of these sites are described in Table 1. The nearest meteorological stations are located 52, 70 and 1 km away from Pichi Ciego, Arroyito and El Encon, respectively. In general, rainfall decreases and temperature increases from Pichi Ciego to Arroyito and from Arroyito to El Encon. The xeric conditions follow a similar trend increasing from Pichi Ciego to El Encon.

Seeds of each variety were sown in seedling boxes filled with sandy-loam soil previously sterilised with methyl bromide. When plants reached an height of 4–5 cm, they were transplanted to 330 cm^3 plastic pots and filled with the same nursery soil. When plants had 4–5 tillers they were transplanted to the experimental field. Physico-chemical characteristics of the soil in the experimental field were: electrical conductivity 785 µS/cm; pH 7.11; N 441 mg/kg (determined by Kjeldhal); P (P_2O_5) 10.4 mg/kg (Jackson 1964); K (K_2O) 1084 mg/kg (Jackson 1964); texture: sandy; field capacity: 0.143 g/g (at a water potential of −0.01 MPa); wilting point 0.07 g/g (at a water potential of −1.5 MPa). Sandy soil is the typical soil where the varieties were collected.

Treatment plots were distributed in a randomized block-design with 8 replications. Each plot had an area of 10.50 m^2, with 14 plants, 1.00 × 0.75 m apart to prevent any competition among plants. Plants were irrigated weekly. Entire plants were harvested 75, 128 and 172 days after being transplanted (DAT). Eight plants from each variety (1 per plot) were harvested on the first and second sampling dates and 2 plants per plot on the last date. Aboveground material was divided into leaf blades, sheaths + culms, and panicles and oven-dried at 70°C until constant weight. Four plants per variety were used for leaf area measurement using a leaf area meter (Li-Cor Mod. 3000A, Li-Cor, Lincoln, NE) and determination of DM. A regression

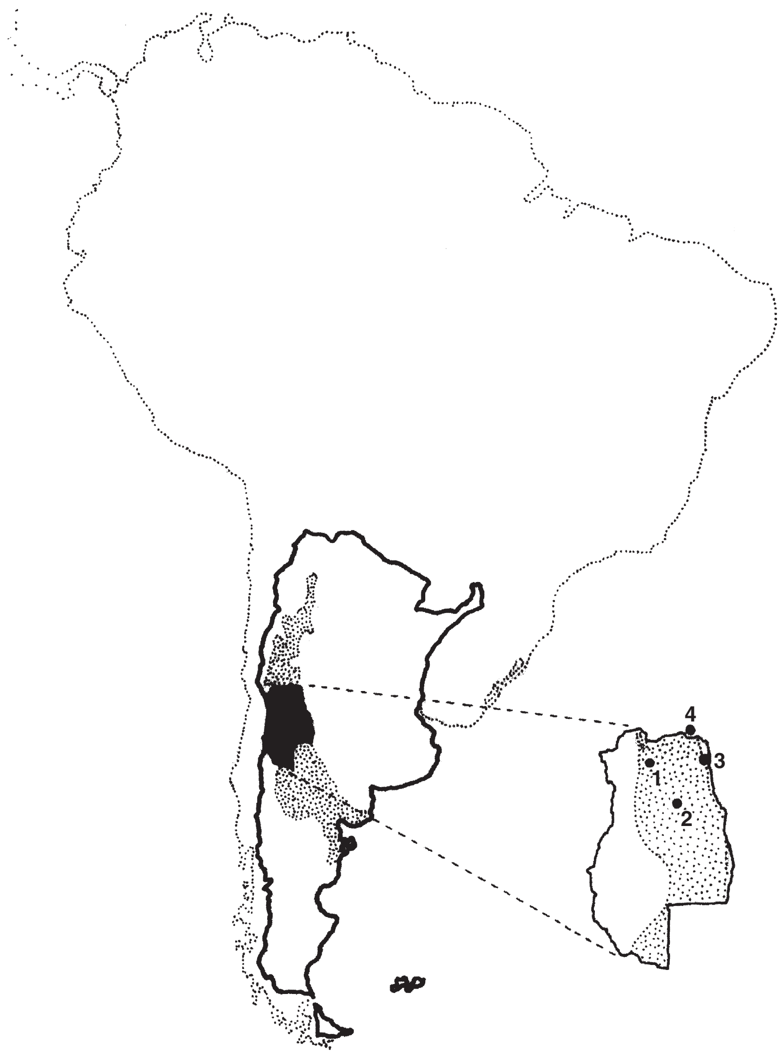

Fig. 1. Map showing the phytogeographical Monte province of Argentina (shaded area), and the locations of: experimental field (1), and site of collection of varieties Pichi (2), Arroyito (3) and Encon (4).

Table 1. Climatic and soil characteristics of the sites of origin of three *Trichloris crinita* varieties (Pichi, Arroyito and Encon)

Attribute	Pichi Ciego	Arroyito	El Encon
Altitude above sea level (m)	610	506	530
Annual mean precipitation (mm)	324	258	104
Annual mean temperature (°C)	15.6	16.7	18.3
Mean minimum temperature of the coldest month (°C)	−0.5	−0.5	−0.1
Mean maximum temperature of the hottest month (°C)	32.6	34.7	34.4
Mean period without frost (days)	120	155	181
N content (mg/L)[A]	560	644	532
P (P_2O_5) content (mg/L)	5.83	6.49	5.34
K (K_2O) content (mg/L)	819	832	872
Organic matter content (%)	0.20	0.26	0.29

[A]N determined by Kjeldhal; P and K according to Jackson (1964).

equation between the two variables was calculated. Subsequent leaf areas values were estimated using the varieties' leaf DM values and the corresponding equation.

We calculated most of the parameters used in quantitative analysis of plant growth (Evans 1972; Hunt 1978) to investigate which of them explain best differences in DM production of the varieties.

The parameters were calculated for the periods corresponding to the three sampling dates, according to the classical approach (Hunt 1978).

RGR (relative growth rate) = increase in plant DM per unit DM and unit time (mg/g.day).
NAR (net assimilation rate) = increase in plant DM per unit leaf area and unit time (g/m.day).
LAR (leaf area ratio) = plant leaf area/plant total DM (m^2/g).
SLA (specific leaf area) = leaf area/leaf DM (m^2/g).
LWR (leaf weight ratio) = leaf DM/plant DM (g/g).
LARD (leaf area rate development) = increase in leaf area per unit time (mm^2/day).

Roots were collected by washing the soil on top of a 0.6 mm screen. Subsequently the samples were oven-dried at 70°C. On the first sampling date, the total soil volume explored by the roots was used. On the second and third dates (128 and 172 DAT), soil samples were obtained with a core sampler at 0, 20 and 40 cm from the centre of each plant at 2 depths: 0.0–0.20 m and 0.20–0.40 m, according to Bohm (1979). Total root biomass was obtained by extrapolation of the root biomass from the sampled cores to the total soil volume explored by roots.

ANOVA and Tukey's test at $P \leq 0.05$ was used to compare means. Dry matter data were transformed by log $(x+1)$ (Poorter and Nagel 2000) and LADR by ln to fulfill ANOVA requirements.

Results

Total plant DM of Pichi and Arroyito (Fig. 2) was significantly higher than that of Encon for all sampling dates. Total plant biomass of Encon was only 39% on the first sampling date and 18% on the following sampling dates compared with the most productive variety Pichi (Table 2). Considering shoot DM components, Pichi was higher than Encon for all organs at each date, except for panicles at the first date. Arroyito presented a similar pattern to Pichi. These two varieties showed no differences between them except for blades on the second date (Table 2).

Shoot/root ratio of Encon was significantly lower than the other 2 varieties on the second and third dates (Table 2). This low ratio was associated with a low shoot DM of Encon, since it was only 18% of that observed for Pichi in the final harvest. In contrast, root DM of Encon on the same date (60.2 g/plant), although significantly lower than Pichi, was equivalent to 70% of the latter.

Leaf area values of Pichi and Arroyito (Fig. 3) were higher than Encon for all dates considered. Interestingly, a fast leaf area development was recorded for Pichi, as shown by the slope of the lines between dates and data corresponding to LADR (Table 3). The final leaf area was six times larger in Pichi than in Encon.

Despite the large differences among varieties in DM production on all sampling dates, the varieties' RGRs differed only in the first period (0–75 DAT). Here, RGR was very low at the end of the annual cycle (third period) for all varieties. The varieties did not differ in NAR. Pichi and Arroyito showed significantly higher LAR than Encon for each of the three DAT (Table 3). Also SLA, one of the components of LAR, was higher in the more productive varieties

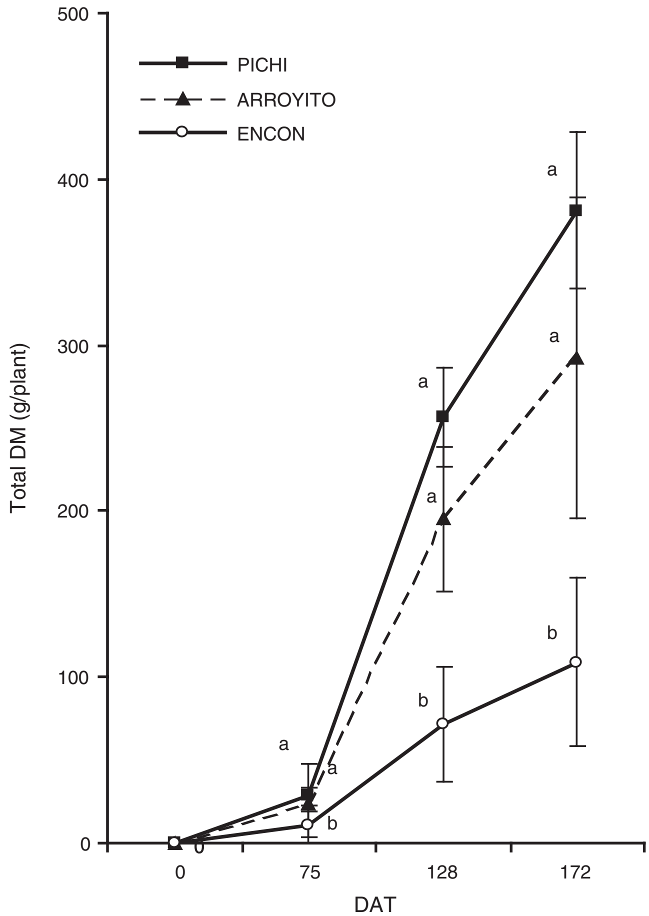

Fig. 2. Changes in total dry matter during vegetation cycle of three varieties (Pichi, Arroyito and Encon) of *Trichloris crinita*. Bars represent ± standard error of the mean. The same letters on each date, indicate non significant differences among varieties according to Tukey's test ($P \leq 0.05$, $n = 8$).

Table 2. Dry matter of different organs (g/plant) and shoot/root ratio of 3 varieties (Pichi, Arroyito and Encon) of *Trichloris crinita* on 3 sampling dates

DAT, days after transplanting. Varieties with the same letter on each date and organ are not statistically different, Tukey test ($P \leq 0.05$; $n = 8$)

DAT	Variety	Shoot DM				Root DM	Shoot/root
		Blades	Sheaths + culms	Panicles	Total		
75	Pichi	7.6a	15.4a	0.8a	23.8a	4.6a	5.2a
	Arroyito	5.7a	13.8ab	1.5a	21.1a	3.1ab	6.8a
	Encon	2.7b	6.4b	0.3a	9.4b	1.9b	4.9a
128	Pichi	54.5a	131.8a	26.5a	212.8a	44.2a	4.8a
	Arroyito	30.6b	100.5a	26.6a	157.7a	38.1a	4.1a
	Encon	10.2c	24.5b	3.5b	38.2b	34.0a	1.1b
172	Pichi	58.3a	189.2a	9.1a	276.6a	85.8a	3.2a
	Arroyito	40.6a	151.6a	34.7a	226.8a	69.7ab	3.2a
	Encon	12.8b	34.3b	3.7b	50.8b	60.2b	0.8b

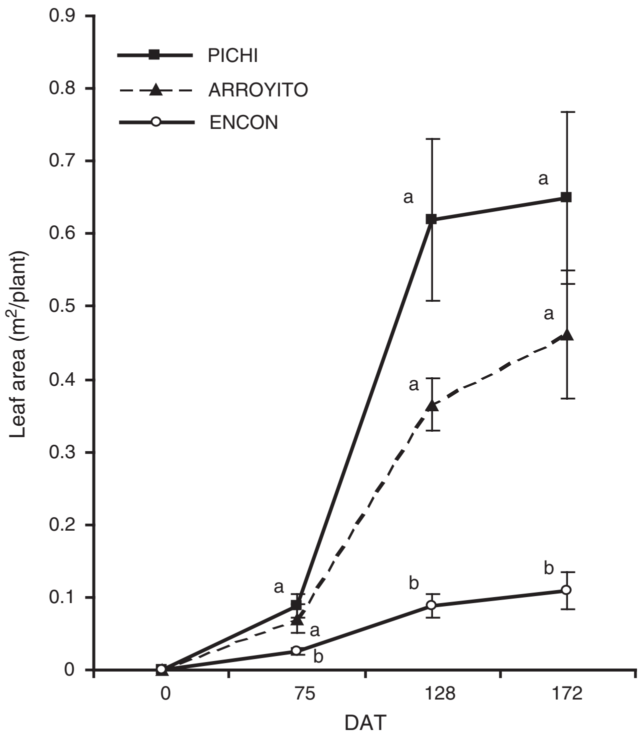

Fig. 3. Changes in leaf area during the growth cycle of three varieties (Pichi, Arroyito and Encon) of *Trichloris crinita*. Bars represent ± standard error of the mean. The same letters on each date, indicate non significant differences among varieties according to Tukey's test ($P \leq 0.05$; $n = 8$).

(Pichi and Arroyito), but leaf biomass, relative to total plant biomass (LWR), was different only on the second date. Significant differences in LADR were found among varieties in the first and second period. The rate of leaf area development of Pichi was eight times higher than that of Encon for this latter period.

The lower biomass and smaller leaf area per plant as well as the lower specific leaf area of Encon, suggests that this variety possesses a less developed photosynthetic area per gram of biomass allocated in the leaves.

Considering DM partitioning to different organs, expressed as the percentage of plant total DM (Fig. 2), we observed differences in partitioning to sheaths + culms, and panicles and roots, but no differences among varieties in the proportion of biomass allocated to leaf blades, was noted. Compared with Encon, that sent more than 60% of the total biomass to roots, Pichi and Arroyito partitioned about 50% of DM to sheaths and culms. Arroyito partitioned the largest proportion to panicles.

Discussion

The results confirmed our hypothesis that the higher aboveground productivity of some varieties of *T. crinita* was due to a larger DM partitioning to shoots than to roots. Varieties Pichi and Arroyito, with high and medium productivity respectively, partitioned more DM to shoots relative to root, as compared with the less productive variety (Encon). We also have shown that the higher total plant biomass produced by Pichi and Arroyito can be explained by a larger leaf area and higher LADR (Fig. 3; Table 3) as postulated in the second hypothesis.

The low DM of Encon can be interpreted in various ways. A first approach is to consider total DM accumulation as a function of the radiation intercepted by the leaves through the conversion of that radiation to dry matter (Monteith 1977). The amount of light intercepted by leaves depends, to a great extent, on the total leaf area developed by a plant, the foliage duration and the morphology and spatial disposition of leaves. The varieties tested here did not differ in foliage persistence, which was 195 days, but they did differ in the production of total leaf area, being significantly lower for the least productive variety. Compared with the other varieties, the rate

Table 3. Measured traits for 3 varieties (Pichi, Arroyito and Encon) of *Trichloris crinita* on 3 sampling dates

Relative growth rate (RGR, g/g.day), net assimilation rate (NAR, g/m^2.day), leaf area ratio (LAR, m^2/kg), specific leaf area (SLA, m^2/kg), leaf weight ratio (LWR, g/g) and leaf area development rate (LADR, mm^2/day). DAT, days after transplanting. Varieties with the same letter on each date and parameter are not statistically different, Tukey test ($P \leq 0.05$; $n = 8$)

DAT	Variety	RGR	NAR	LAR	SLA	LWR	LADR
75	Pichi	73a	18.6a	3.2a	11.9a	0.27a	1189a
	Arroyito	69a	18.0a	3.1a	12.2a	0.25a	929a
	Encon	57b	18.0a	2.4b	9.5b	0.30a	331b
128	Pichi	43a	16.8a	2.3a	11.6b	0.20a	9815a
	Arroyito	45a	20.0a	1.9b	12.1a	0.16b	5466a
	Encon	42a	25.3a	1.2c	9.0c	0.14b	1161b
172	Pichi	9a	5.8a	1.3a	11.4a	0.11a	603a
	Arroyito	7a	5.6a	1.3a	12.0a	0.11a	2063a
	Encon	9a	7.4a	0.7b	8.7b	0.08a	487a

of leaf area development in Encon was also slower (Fig. 3). Thus, both factors could be contributing to a reduced light interception. Similar results were obtained by McNaughton (1974) using varieties of *Typha latifolia*.

The more productive varieties (Pichi and Arroyito) had a higher LAR indicating that they have a larger photosynthetic area per gram of total plant biomass. These results are in agreement with those reported by other authors (Poorter and Remkes 1990; Poorter and Pothmann 1992; Reich 1998). Since LAR = LWR × SLA (Hunt 1978), and since the varieties did not differ in LWR (except for the second date), the differences that we observed in photosynthetic areas do not mean that Pichi and Arroyito invested more biomass in producing leaf blades. Instead, they reflect a larger leaf area per gram of DM invested in leaves (SLA) (Table 3; Fig. 4). These results are in agreement with those of Poorter and Lambers (1991), who found that differences in growth rates among 24 herbaceous species were mainly associated with variations in SLA rather than to differences in LWR. Dijkstra and Lambers (1989), working with two lines of *Plantago major*, and Poorter and Remkes (1990), Garnier (1992), Poorter and Pothmann (1992) and Reich (1998) studying different groups of species came to similar conclusions. A strong correlation between LAR and SLA was also found in herbaceous monocotyledons (Hunt and Cornelissen 1997).

Varieties' RGRs were different only on the first DAT, but this parameter cannot explain the great differences in biomass production during the second one. This may be due to its importance in the exponential phase of growth but later on RGR is not a good indicator for growth (Loomis and Connor 1992). NAR could not explain differences in DM production either.

The least productive variety invested 60% of its biomass in roots, while the other two invested mainly in sheaths + culms. The larger proportion of roots in Encon suggests less efficiency in the use of radiation because of greater respiratory losses by roots; contrarily, the large proportion of sheaths + culms in Pichi and Arroyito would mean an extra contribution of assimilates through photosynthesis by these organs. In an experiment with *Agropyron*, Caldwell *et al*. (1981) showed that sheaths + culms contributed more than 50% to the total photosynthesis.

The hypothesis concerning differential assimilate partitioning to organs in forages was based on differences in productivity found among old and modern cultivars (Gifford *et al*. 1984). In such crop species, productivity increased as harvest index increased. In the case of *Trichloris crinita*, the harvest index (considered as shoot DM) was also higher for those varieties with higher productivity. However, considering that this is a native forage species where no breeding programs have been carried out it is expected that varieties have evolved achieving an optimal shoot/root ratio,

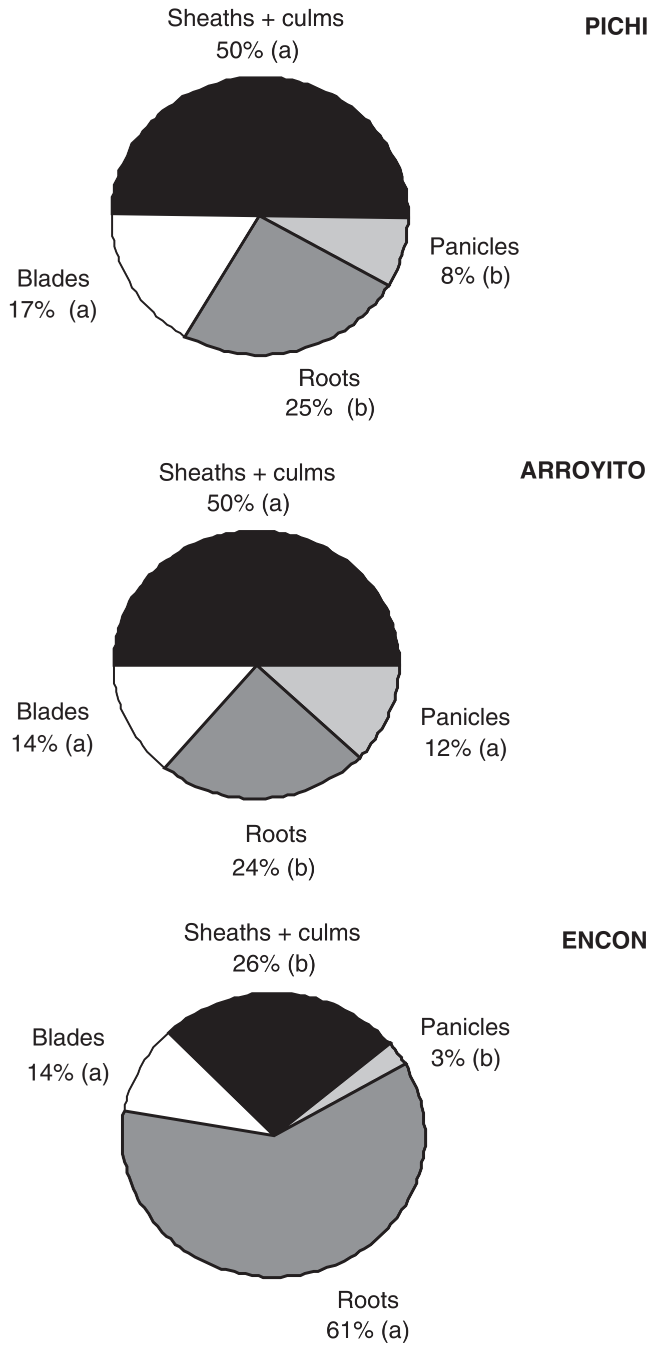

Fig. 4. Dry matter partitioning to different organs, as a percentage of total dry matter, in the last sampling date for three varieties (Pichi, Arroyito and Encon) of *Trichloris crinita*. The same letters for each organ indicate non significant differences among varieties according to Tukey's test ($P \leq 0.05$; $n = 16$).

thus increasing their adaptation to the native environments (Gleeson and Tilman 1992).

Our results showed that the lower biomass production by Encon plants is associated with smaller leaf area, slower leaf area development, less developed photosynthetic area per gram of biomass produced, and probably higher respiratory cost due to a larger proportion of roots. All these traits can be interpreted as adaptations to the more xeric conditions found in its area.

Increased root/shoot ratio can be the consequence of nutrient deficiency, lack of water in the soil, or temperatures unfavourable for optimal root functioning (Brouwer and de Wit 1969; Poorter and Nagel 2000). Therefore, we can speculate that the larger investment in root biomass observed in Encon might represent a physiological mechanism adapting this genotype to its native area of scarce rainfall (104 mm/year) high temperatures (18.3°C mean annual temperature) and nutrient-deficient soils (see Tables 1 and 2). Under these conditions, a larger root system will assure a better exploitation of soil resources (water and nutrients), while a limited leaf area development would be advantageous for avoiding water losses through transpiration. Both types of adaptations could increase survival in such a dry and rather unfertile site (Grime 1979). Similarly, along an aridity gradient in Patagonia, Schulze *et al*. (1996) found that plant total biomass decreased as precipitation decreased, but belowground biomass decreased at a lower rate than aboveground biomass, resulting in increasing root/shoot ratios. Fernández and Reynolds (2000) studying growth parameters and drought tolerance in eight desert grasses did not find a trade-off between total biomass or root/shoot ratios and drought tolerance. Instead, in this experiment, the increases in the root/shoot ratio showed by Encon implied a trade-off in total dry matter production.

The lower SLA of Encon is another trait associated with an adaptation to arid conditions, according to Tsunoda (1978).

Congruently, Pichi, which has a larger leaf area and a smaller proportion of roots, comes from an area with higher rainfall and lower temperatures (324 mm/year and 15.6°C mean annual temperature). This feature allows Pichi plants to achieve a very high biomass production whenever appropriate temperatures and rainfall are available, as this occurs more often in the region where this variety belongs (Seligman *et al*. 1992).

These results will benefit future programs oriented to the re-vegetation of degraded areas of the Monte by providing an objective means for choosing varieties – based on productivity and adaptation – suitable for different environments within the Monte region.

In summary, the largest above ground productivity of PICHI is associated with higher shoot/root ratio and higher total DM production, which, in turn, is due to a larger leaf area production and higher rate of leaf area development. These traits have evolved in areas of the Monte with lower temperatures and higher rainfall. Instead, under more xeric conditions (higher temperature and lower rainfall) plants have evolved to have a lower leaf area and a higher root/shoot ratio allowing, thus, a more thorough soil exploration with a more extended root system. These seem to be among the best adaptations to couple with severe drought conditions, as observed in the variety Encon.

Acknowledgments

This research was supported by CONICET and Universidad Nacional de Cuyo, Argentina. We thank Dr A. H. Hall and Dr Kent Bradford for their comments on the manuscript. We are grateful to H. Morales for his valuable technical assistance, and to N. Horak, J. Lucero, M. Delugan and M. Paez for their kind collaboration.

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Manuscript received 15 September 2004, accepted 12 April 2005