REVIEW ARTICLE

Exploiting genetic and physiological variation of the native forage grass *Trichloris crinita* for revegetation in arid and semi-arid regions: An integrative review

P. C. Kozub[1] | J. B. Cavagnaro[1] | P. F. Cavagnaro[2,3,4]

[1]Facultad de Ciencias Agrarias (FCA), Instituto de Biología Agrícola de Mendoza (IBAM), Consejo Nacional de Investigaciones Científicas y Técnicas (CONICET), Universidad Nacional de Cuyo (UNCuyo), Mendoza, Argentina

[2]Instituto Nacional de Tecnología Agropecuaria (INTA) EEA La Consulta, La Consulta San Carlos, Provincia de Mendoza, Argentina

[3]Consejo Nacional de Investigaciones Científicas y Técnicas (CONICET), Mendoza, Argentina

[4]Facultad de Ciencias Agrarias, Instituto de Horticultura, Universidad Nacional de Cuyo, Mendoza, Argentina

Correspondence
P. F. Cavagnaro, Instituto Nacional de Tecnología Agropecuaria (INTA) EEA La Consulta, La Consulta San Carlos, Provincia de Mendoza, Argentina.
Email: pablocavagnaro@hotmail.com

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Abstract

In arid, semi-arid and dry subhumid regions, which represent ∼ 41% of the Earth's land surface, desertification and soil degradation are very frequent, leading to low soil fertility and productivity. In these regions, revegetation with locally adapted native species may aid in ameliorating desertification processes. *Trichloris crinita* is a C4 perennial grass native to arid and semi-arid regions of the American continent. Its good forage quality, drought tolerance, resistance to trampling and grazing, and rapid growth and competing aggressiveness among other native species warrant its use as forage and for revegetation purposes. In the last decades, many studies have revealed broad intraspecific genetic variation for ecophysiological, morphological, biomass production, nutritional quality (as forage) and adaptive stress response-related traits. Also, results from field trials evaluating *T. crinita* genotypes as forage and for restoration of degraded areas suggest great potential for—and have encouraged—its utilization under different habitats and environmental conditions. In this integrative review, we compiled and discussed the most relevant research data regarding *T. crinita*, focusing on aspects and traits that influence its utilization both as forage and in rehabilitation of degraded lands. Challenges and prospects towards the improvement of this species in breeding programmes with specific goals are discussed.

KEYWORDS
biomass production, drought tolerance, forage grass, genetic variation, molecular markers, *Trichloris crinita*

1 | INTRODUCTION

1.1 | Importance of developing forage and revegetation grasses for arid and semi-arid regions

Dry lands—which include arid, semi-arid, and dry subhumid areas—cover nearly 41% of Earth's land surface and are home to more than 38% of the total global population (Global Land Project, 2005; Millennium Ecosystem Assessment, 2005). Severe land degradation is present on 10–20% of these lands, whose consequences directly affect ∼250 million people, mainly in developing countries (Millennium Ecosystem Assessment, 2005). These estimates are likely to increase in the following years, because of climate change and population growth. According to Khagram, Clark, and Raad (2003), dry land populations are among the most ecologically, socially and politically marginalized societies on Earth.

Land desertification, along with low fertility and low organic matter content in the soils, is very frequent in arid and semi-arid regions. These factors, along with global climate change, mining and

excessive ploughing, promote the loss of biodiversity and soil productivity (Bedunah & Angerer, 2012; Harris, 2010; Zhang, Wang, Zhao, Xie, & Zhang, 2005). In addition, tillage and overgrazing by domesticated animals can rapidly worsen the situation leading to increased soil degradation (GLP, Global Land Project, 2005; Papanastasis, 2009). It is estimated that 20–73% of the world's grazing areas are moderately to severely degraded, according to assessments performed in different studies (reviewed by Lund, 2007). Moreover, loss of perennial grasses in rangelands, often accompanied by severe soil erosion and salinity, is a frequent component of desertification processes in many arid and semi-arid regions (Waters & Shaw, 2003). Altogether, these data indicate that land degradation is a widespread phenomenon and regarded as a global concern (Harris, 2010).

The strategy to address these degradation issues has traditionally been to reseed the degraded areas with introduced perennial species. However, in the last decades the trend has moved towards the use of native species, with a clear recognition of their intrinsic adaptive and ecological value (Waters & Shaw, 2003). Several examples of application of this strategy can be found in revegetation programmes of Australia and North America. For example, in North America, seeds of a number of regionally adapted cultivars of native grass species that are easily grown in cultivation are commercially available in fairly large quantities. However, seed of native species that are less easily cultivated, or more geographically restricted, can rarely be purchased (Dickerson & Wark, 1997; May, Wark, & Coulman, 1997; Smith & Whalley, 2002). In Australia, several cultivars from 12 locally adapted native grass species have been developed—for revegetation purposes —and commercialized by the Australian native seed industry (Cole & Johnston, 2006; Waters, Whalley, & Huxtable, 2000).

The development of locally adapted cultivars of native grass species is crucial for their successful utilization as forage and in revegetation programmes. Germplasm characterization for interesting forage-related traits (e.g., biomass production, protein content and quality, palatability, tolerance to grazing) and revegetation-related traits (e.g., tolerance to drought and salinity, seed yield, competing aggressiveness) is a prerequisite for the selection and development of improved native grass cultivars. In this review paper, we compiled and critically discussed the most relevant data published to date regarding *Trichloris crinita*, with particular emphasis on its extremely broad intraspecific genetic variation found for forage- and revegetation-related traits.

1.2 | Taxonomy

Trichloris is a native American genus represented by two species, *Trichloris crinita* (Lag.) Parodi and *Trichloris pluriflora* E. Fourn. Both are C4 perennial grasses belonging to the Cynodonteae tribe of the Chloridoideae subfamily, within Poaceae.

The taxonomic classification of *Trichloris* within the Chloridoideae subfamily has been controversial. Initially, some authors considered *Trichloris* and *Chloris* as synonymous genera (Anderson, 1974; Clayton, 1967), based upon morphological similarities between some Australian *Chloris* species and *Trichloris*. According to Nicora and de

Rúgolo Agrasar (1987), *Chloris* and *Trichloris* present distinct morphological traits that justify their classification as separate genera. Later molecular studies also separated the species of *Trichloris* from *Cloris* (Hilu & Alice, 2001 Cavagnaro, Cavagnaro, Lemes, Masuelli, & Passera, 2006; Peterson et al., 2012; 2015). More recently, results from phylogenetic analyses with extensive taxon sampling using plastid and nuclear DNA sequences placed *T. crinita* and *T. pluriflora* in the genus *Leptochloa* and renamed them as *Leptochloa crinita* and *Leptochloa pluriflora*, whereas nearly all the *Chloris* accessions formed a well-supported and separate clade from *Leptochloa* (Peterson et al., 2012; 2015).

1.3 | Botanical description

The main morphological characteristics of *T. crinita* are presented in Figure 1. The plants are perennial and caespitose, decumbent or upright, of approximately 20–40 cm tall in vegetative stages, and 50–90 cm after inflorescences are set. They produce dense inflorescences composed of digitate racemes, solitary and small spikelets with one sterile floret and a fertile one below. Glumes are lanceolate, laterally compressed, pubescent and persistent, with the upper glume apex being acuminate and composed of three awns, the central awn longer than the laterals awns (Anton, Zuloaga, & de Rúgolo Agrasar, 2012; Kozub et al., 2017). Lack of cleistogamous spikelets was reported in a recent study that analysed ~ 2,000 spikelets from 20 *T. crinita* accessions (Kozub et al., 2017). Flowering occurs downwards, from the apex to the basal spikelets of the inflorescence. In two days, anthesis is complete in the inflorescence. Anthesis occurs between 7:00 and 11:00 h.

The floral characteristics of *T. crinita* are typical of selfing species. It displays floral traits such as short floral life spans, small flowers and small anther–stigma separation (Duncan & Rausher, 2013). The general pattern of floral development observed in this species is similar to that described for other self-pollination grasses, including small millets (Gupta, Sood, Agrawal, & Bhatt, 2012) and many Australian native grasses (Whalley, Chivers, & Waters, 2013). Dense inflorescences and profuse flowering, as reported in *T. crinita* (Kozub et al., 2017), are believed to favour selfing and probably cause a certain amount of spontaneous self-pollination by geitonogamy (Barrett, 2003).

The main morphological difference separating the two *Trichloris* species is that *T. crinita* has spikelets with two flowers and lemmas with three awns of the same length, whereas *T. pluriflora* has spikelets with three to five flowers and lemmas with its central awn twice the size of the lateral awns. *Chloris* species have only one awn per floret (Hitchcock, 1971; Nicora & de Rúgolo Agrasar, 1987).

1.4 | Geographical distribution

The species presents an amphitropical disjunct distribution (Peterson, Columbus, & Pennington, 2007) in arid and semi-arid rangelands of South and North America, as depicted in Figure 2. *Trichloris crinita* naturally grows in warm temperate regions of America including the south of United States, North of Mexico, and in South America in
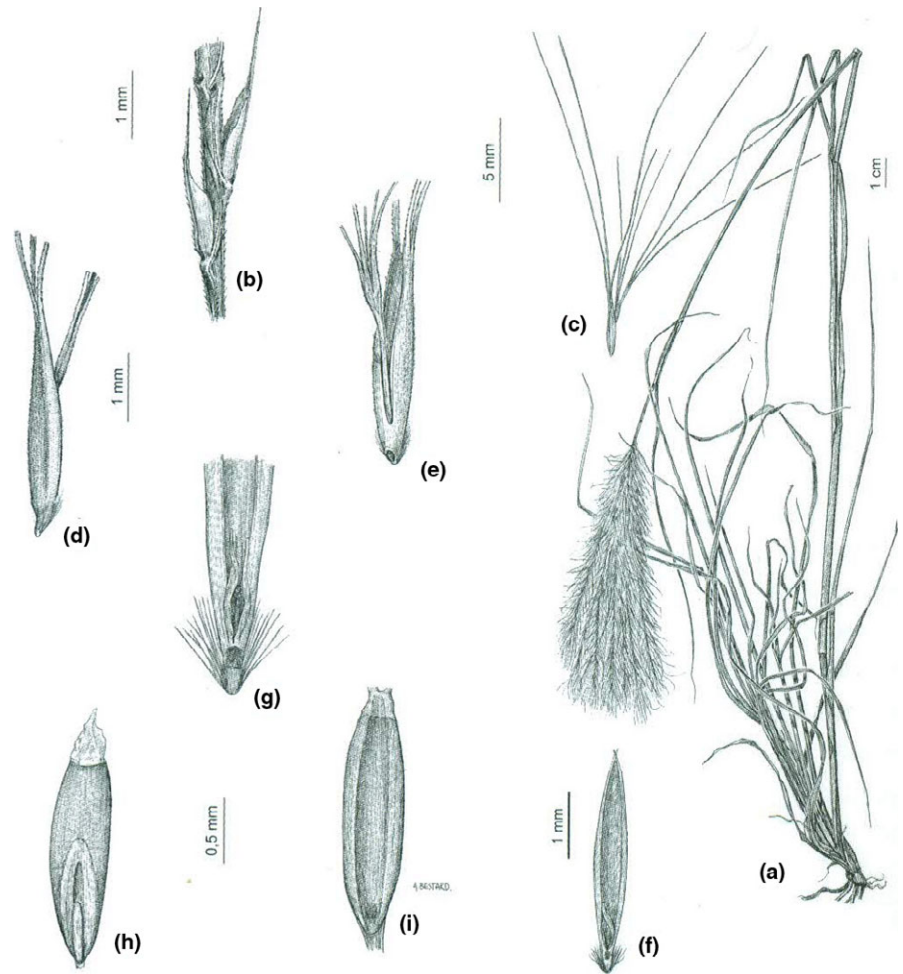
FIGURE 1 Plant morphology of *Trichloris crinita*. (a) Whole plant, (b) rachis with glumes, (c) floret, (d) floret (lateral view), (e) floret (ventral view), (f) palea (ventral view), (h) caryopsis (scutellar view), (i) caryopsis (hilar view). Figure adapted from Anton et al. (2012)

Paraguay, Bolivia, Chile and Argentina, being scarce in Uruguay (Anton et al., 2012). In Argentina, *T. crinita* is abundantly found in warm environments of the phytogeographical province of Monte, Chaco and Espinal (Cabrera, 1994). It behaves as a typical warm-season species, growing whenever soil water is available and the temperature is above 10°C (Seligman, Cavagnaro, & Horno, 1992). The species can be found up to 1500 metres above sea level (Cavagnaro, 1988). In its natural habitat of Monte, *T. crinita* is commonly found interspersed with other C4 herbaceous species, shrubs of the genus *Larrea*, and a few tree species, mostly of the genus *Prosopis* (Cabrera, 1976).

1.5 | Chromosome number and ploidy level

Polyploidy in Chloridoideae is highly frequent. According to Fedorov (1969), *T. crinita* is tetraploid ($2n = 4x = 40$) and *T. pluriflora* is hexaploid ($2n = 6x = 60$). These data derived from simple mitotic chromosome counts and assuming the same basic chromosome number ($x = 10$) as reported in other species of the Chloridoideae subfamily. Recent data from analysis of chromosomes pairing during meiosis revealed, in all cases, 20 bivalents, suggesting that *T. crinita* is an allotetraploid with disomic inheritance (Kozub et al., data in preparation). This information is very relevant for developing future breeding programmes in this species, as breeding strategies used in an allotetraploid with disomic inheritance differ greatly from those

applied in autotetraploids with polysomic inheritance. These two types of polyploidy have very distinct features that affect the selection of proper breeding strategies. For example, disomic allopolyploids are usually fertile and frequently self-compatible. On the other hand, polysomic autopolyploids may exhibit reduced fertility due to irregular chromosome conformations in meiosis, tend to be self-incompatible, generally present high inbreeding depression upon self-fertilization and complex inheritance patterns.

Fluorescent and genomic *in situ* hybridizations (FISH and GISH) may help confirm allotetraploidy in *T. crinita* and identify its ancestral progenitor species. Studies of this type have been performed in other Chloridoideae, such as *Cynodon* (Brilman, Kneebone, & Endrizzi, 1982) and *Eleusine* (Bisht & Mukai, 2000).

1.6 | Mode of reproduction

Genetic studies and breeding of *T. crinita* have been very limited, partly as consequence of the lack of knowledge on its mode of reproduction. Apomixis or autogamy was initially proposed as the species mode of reproduction based upon the recurrent observation that the entire progeny of a plant had the same phenotype as the mother plant (Cavagnaro et al., 2006).

Very recently, Kozub et al. (2017) and Gutiérrez, Richard, and Cerino (2016) determined that *T. crinita* reproduces by means of
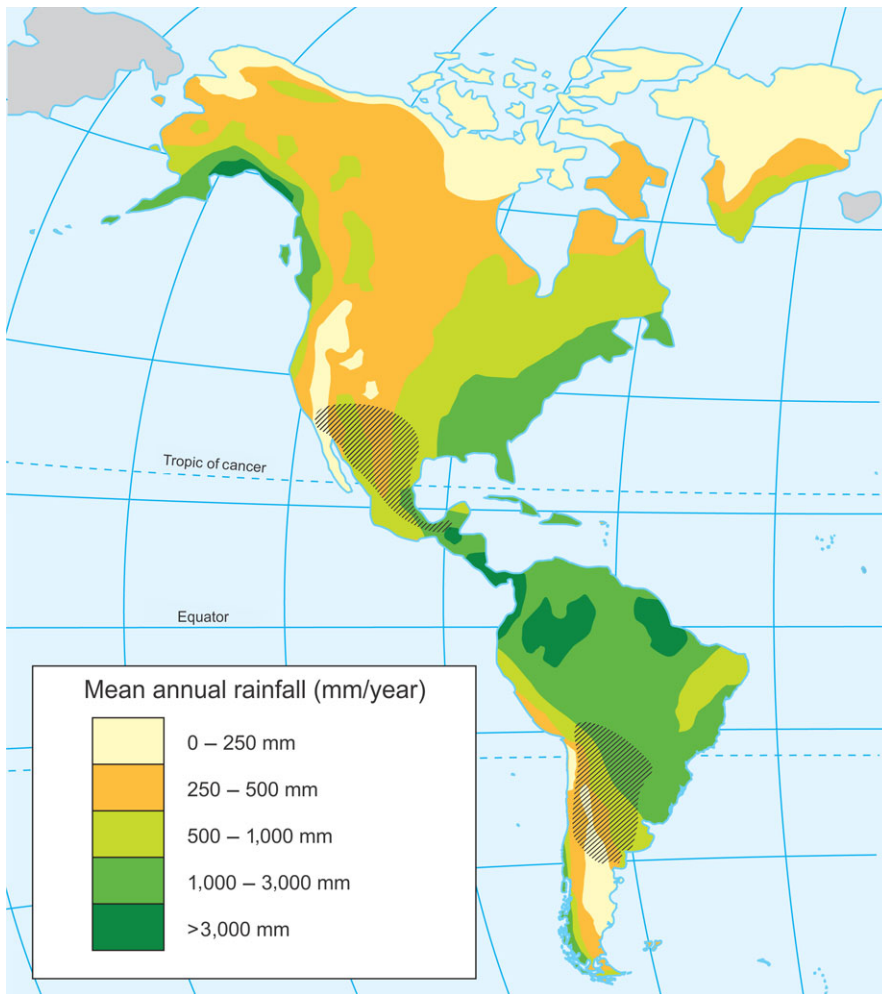
FIGURE 2 Geographical distribution of *Trichloris crinita* and *Trichloris pluriflora* in America (stripped area) with isohyets

sexuality, being the species self-compatible and autogamous. Sexuality was determined through embryological analyses in both studies. Gutiérrez et al. (2016) performed cytological observations in *T. crinita* inflorescences collected at the beginning of emergence and observed that megasporogenesis takes place at this stage, and they described the morphology of the mature megagametophyte. Kozub et al. (2017) analysed, cytologically, 1,400 ovules from 20 different *T. crinita* accessions, finding that all the accessions had a single megagametophyte per ovule and that the embryo sac was eight nucleate and consisted of seven cells: the egg cell and two synergids at the micropylar pole, the central cell (with two polar nuclei) and three antipodal cells at the chalazal pole. The authors used flow cytometry seed screen (FCSS) to further analyse the origin of the embryo sac (sexual or apomictic) and showed 2C and 3C DNA contents for embryo and endosperm tissues respectively. The combined data from embryo sac and FCSS analyses, reported by Kozub et al. (2017), conclusively demonstrated that *T. crinita* seeds develop sexually (i.e., through double fertilization). In addition, pollination experiments performed in both studies concluded that *T. crinita* is self-compatible, because all the plants analysed produced seeds under self-pollination conditions (Gutiérrez et al., 2016; Kozub et al., 2017). In these studies, self-pollination was

ensured by isolating inflorescences in moderately transparent paper bags 2 days prior to anthesis.

By progeny testing and molecular marker analyses using simple sequence repeats (SSRs), Kozub et al. (2017) determined that *T. crinita* is predominantly—if not exclusively—autogamous, as all the progenies evaluated had the same maternal phenotype, for various morphological traits analysed, and the same maternal SSR genotype. The same results were found when reciprocal crosses were analysed. Mean observed heterozygosity (H_o) per locus was 0.46, whereas expected heterozygosity (H_e) per locus was 0.56 in average. Eight of the 16 SSR loci analysed had $H_o = 0$, $H_e = 0$ and one allele per locus; i.e., all the accessions were homozygous and showed a single allele for these polymorphic loci. Estimates of F_{IS} for each locus were positive in most of the loci analysed, whereas multilocus F_{IS} was also positive with a mean value of 0.284. The positive values of F_{IS} confirm that *T. crinita* is autogamous.

Altogether, the above data from the recent studies of Gutiérrez et al. (2016) and Kozub et al. (2017) provide conclusive evidence that *Trichloris crinita* reproduces mainly—if not exclusively—by sexual reproduction, and it self-compatible and autogamous.

TABLE 1 Biomass production of *Trichloris crinita*

Origin of *T. crinita* populations	Mean annual rainfall (mm)	Max. biomass (g DM/m²)	Min. biomass (g DM/m²)	Mean biomass (g DM/m²)	Planting density (plants/ha)	References
Mendoza, La Rioja, Catamarca	270, 460, 458	266	34	150	15,625	Cavagnaro et al. (2006)
Catamarca, La Rioja, La Pampa	458, 460, 550	664	68	366	40,000	Gil Báez et al. (2015)
n.d.	n.d.	n.d.	n.d.	202	n.d.	Namur et al. (2011)
Tucumán	525	n.d.	n.d.	324	n.d.	Díaz et al. (1970)

n.d., no data available.

1.7 | Germplasm banks of Trichloris crinita and related taxa

Worldwide, three germplasm banks maintain collections of *Trichloris crinita*. Plant materials are publicly available, in limited amounts, upon request.

1. *National Plant Germplasm System (NPGS)—United States Department of Agriculture (US)*. This cooperative organization run by public (state and federal) and private institutions contains a large number of diverse plant species, including seven accessions of *T. crinita* from four countries and one accession of *T. pluriflora*. Information for several morphological, growth, phenological, and production descriptors, as well as collection sites and dates, is available at the Germplasm Resource Information Network (GRIN) of NPGS (URL: http://www.ars-grin.gov/). Seed can be requested through the GRIN web site.

2. *Germplasm Bank of Native Grasses (GBNG), at the Instituto Argentino de Investigaciones de Zonas Áridas (IADIZA) (Argentina)*. GBNG-IADIZA was created with aim of collecting, preserving, studying and distributing germplasm of native grasses from the Monte region of Argentina. This germplasm originated from plant materials obtained from 48 natural *Trichloris crinita* populations collected all over 350,000 km² of the Monte region. Currently, there are 21 accessions of *Trichloris crinita* conserved in field collections and seed banks. Data concerning the collection sites (geographical references, soil, topography, plant communities), physiognomy, and phenology, as well as morphological, physiological and agronomic characterization of the accessions are available in Lemes (1992) and Cavagnaro et al. (2006).

3. *Facultad de Ciencias Agrarias, Universidad Nacional del Litoral (FCA-UNL) (Argentina)*. The germplasm bank contains 40 accessions of *T. crinita* and 22 of *T. pluriflora* corresponding to populations collected in Argentina. Data about collection sites can be found in Marinoni, Bortoluzzi, Parra-Quijano, Zabala, and Pensiero (2015).

2 | FORAGE BIOMASS PRODUCTION

Trichloris crinita is a summer-growing perennial grass tolerant to trampling and grazing by domestic and wild animals, with good forage quality suitable for raising livestock in arid zones (Silva Colomer, Cavagnaro, Lemes, & Medero, 1989; Wainstein & Gonzalez, 1969).

Range grazing is one of the few economic activities in arid and semi-arid regions, and native grasses constitute the main forage resources in these ecosystems. Due to the importance of *T. crinita* for range grazing and the relevance of biomass production in forage species, many studies have evaluated different populations and/or accessions of *T. crinita* based on their biomass production (Cavagnaro et al., 2006; Díaz, Lagomarsino, Prete, & Rodríguez J.C, 1970; Gabutti et al., 2011; Gil Báez, Ordinola Agüero, Ernst, & Ruiz, 2015; Quiroga, 2011). All of them reported broad variation in biomass production among the materials evaluated, with values ranging from 34 to 664 grams of dry matter per square metre (g DM/m²) (Table 1). The study of Cavagnaro et al. (2006) was the only one that characterized *T. crinita* accessions for their biomass production under experimental field conditions, using different location sites and three growing seasons. The study reported broad and significant variation in biomass production, varying almost ninefold between the most productive accession and the least productive one (Figure 3), with mean values ranging from 34 to 265 g DM/m². The relative performance of high-, medium- and low-yielding accessions was consistent over three years and three sites (three environments) suggesting a genetic basis for this trait. Indirect data suggest a strong genetic component for this quantitative trait, as indicated by the genetic clustering of 20 *T. crinita* accessions according to their biomass production (Cavagnaro et al., 2006). As presented in Figure 4, clustering analysis using a large number (~930) of AFLP markers clearly separated *T. crinita* accessions with high (>110 g DM/plant), medium (75–100 g DM/plant) and low (<75 g DM/plant) biomass. Inheritance and linkage studies, including the estimation of heritability values and the genetic mapping of loci (QTL) controlling this trait, are necessary to further explore the genetic basis of biomass production in this species.

Greco (1996) and Greco and Cavagnaro (2005) investigated the relationship among some physiological traits and biomass production in *T. crinita*. Their results indicate that higher above-ground biomass productivity was mainly due to a larger partitioning of photosynthates to shoots, rather than to a higher net photosynthesis rate. In addition, the higher total dry matter (i.e., aerial plus underground biomass) was associated with a higher rate of leaf area development, a larger total leaf area, and a particular morphology and spatial
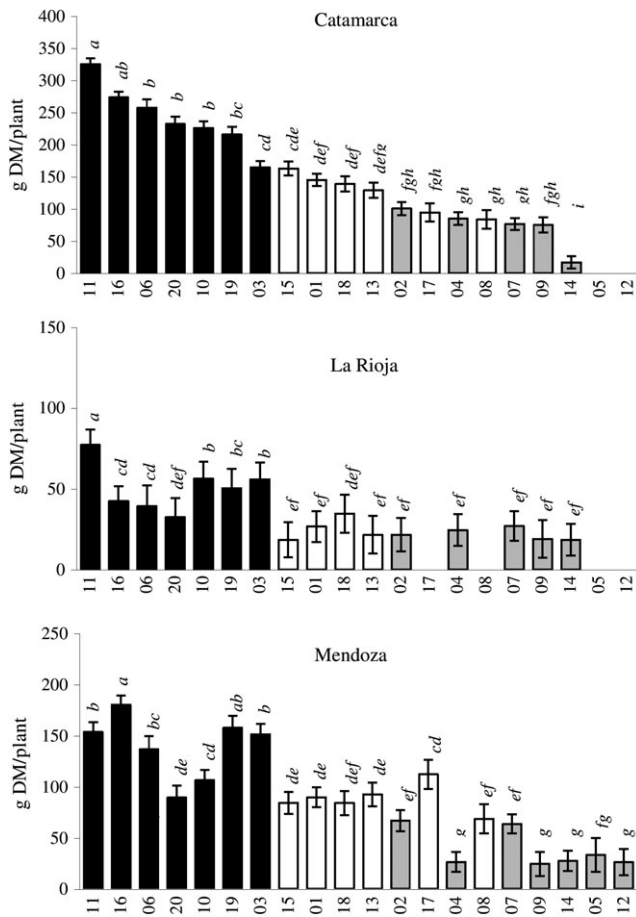
FIGURE 3 Biomass production of 20 *Trichloris crinita* accessions evaluated in three locations (Catamarca, La Rioja and Mendoza) and 3 years. Values are means of three-year data. Black, white and grey bars represent accessions with high (>110 gDM/plant), medium (between 75 and 110 gDM/plant) and low (<75 gDM/plant) biomass yield considering their overall performance in the three locations. Error bars ± standard error. Bars with the same letters are not significantly different at $p \leq .05$, LSD test. Figure from Cavagnaro et al. (2006)

disposition of leaves, which allowed a larger amount of light to be intercepted by leaves. Conversely, low biomass production was associated with smaller leaf area, slower leaf area development and higher respiratory cost due to a larger proportion of roots. All these traits are probably adaptations of accessions to the environmental conditions of their sites of origin.

Direct comparison of biomass production in *T. crinita* with other grass species may be challenging, mainly due to the fact that the published studies using different species were performed under different environmental conditions. Only one study (Cavagnaro, Dalmasso, & Candia, 1983) compared biomass production among several grasses (*Trichloris crinita*, *Pappophorum caespitosum*, *Setaria leucopila*, *Digitaria californica*, *Sporobolus cryptandrus*) under the same environmental conditions (i.e., natural populations) in the arid Monte region of Argentina. Among these, *T. crinita* (150 g DM/plant/year) and *P. caespitosum* (144 g DM/plant/year) had the highest biomass

production, whereas the rest of the species had <60 g DM/plant/year (Cavagnaro et al., 1983).

3 | FORAGE QUALITY

For establishing reliable comparisons in forage quality parameters among species, standardized sampling (and analytical) procedures of plants growing contemporarily under the same environmental conditions must be used. A comparative analysis of crude protein (CP) content in native forage species that coexist in natural populations of an arid region of Argentina (Ñacuñan, Mendoza) revealed lower mean protein content in plants of *T. crinita* (10%) and *Pappophorum caespitosum* (10.6%) than in *Chloris* spp. (11%), *Setaria* spp. (12%) and *Tragus berteroanus* (12.7%) (Wainstein & Gonzalez, 1969). The lower CP content found in *T. crinita*, as compared to these other species, is in agreement with the general inverse association between biomass production and forage quality, as *T. crinita* yields significantly more biomass than the former species (Cavagnaro et al., 1983). However, *T. crinita* has higher CP levels than *Digitaria californica* (5.6%) and *Sporobolus cryptandrus* (6.5%), two other forage species commonly found in semi-arid regions of Argentina (Chirino, Grahn, & Robles, 1988).

Significant variation was found among *T. crinita* accessions for various forage quality parameters, including crude protein, which ranged from 8 to 10.2%, protein linked to fibre, dry-matter solubility and cell wall components (neutral detergent fibre, acid detergent fibre and acid detergent lignin) (Silva Colomer et al., 1989). These data suggest a genetic component conditioning forage quality, and the variation found can be exploited for improving this trait. Despite its genetic component, nutritional parameters of *T. crinita* (and other grasses) are environmentally influenced and tend to show significant interactions involving seasons, years and range conditions (Cerqueira, Sáenz, & Rabotnikof, 2004). It must be noted that all the accessions analysed by Silva Colomer et al. (1989) had CP contents suitable for livestock production (Cerqueira et al., 2004), even at a deferred stage (ARC, 1980). In addition, the nutritional content of this forage species satisfied the maintenance requirements for protein and energy of grazing cows (ARC, 1980).

In conclusion, *T. crinita* has good forage quality for a native grass of arid regions, characterized by a mean CP content of ∼ 9.1%, and a range of variation (genotype-dependent) of 8–10.2%. Although its CP content is not the highest among the native grasses that naturally cohabitate with *T. crinita*, the higher biomass production of the latter translates to a much higher CP yield per hectare. In addition, *T. crinita* has good palatability throughout the growing season. The variation found among *T. crinita* accessions for various forage nutritional parameters can be exploited for improving this trait. Further analyses of nutritional quality in other genetically diverse collections of this species may help identify and select superior genotypes for forage purposes.

FIGURE 4 Phenetic relations among 20 *Trichloris crinita* accessions from UPGMA cluster analysis of the Jaccard similarity coefficient matrix generated using data from 930 polymorphic AFLP bands obtained with 24 primer combinations. Roman numbers indicate groups discriminated at 65% similarity. An accession from *Chloris virgatum* was included in the analysis, as a putative outgroup. Taxa are indicated by the accession number followed by a letter indicating whether they have high (H, >110 g DM/plant), medium (M, from 75 to 100 g DM/plant) or low (L, <75 g DM/plant) biomass yield. Figure from Cavagnaro et al. (2006)
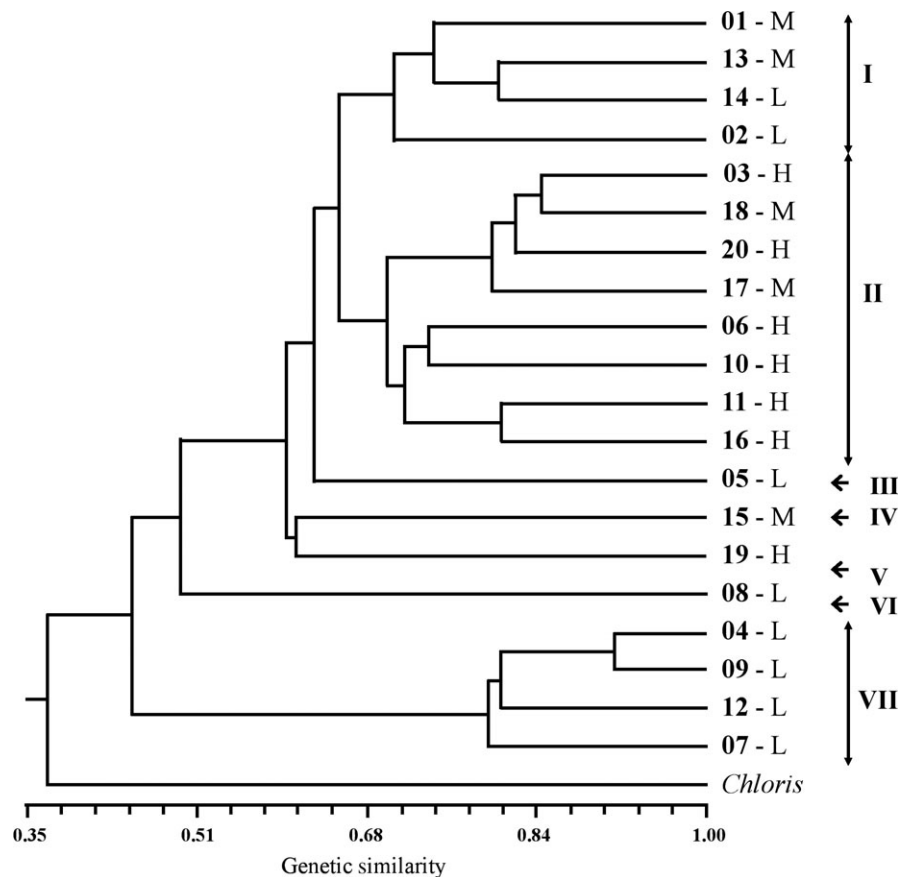
4 | DROUGHT TOLERANCE

In native forage species of arid regions, evaluation of germplasm for drought tolerance is important for the identification and selection of genotypes suitable for revegetation purposes and the design of sustainable management practices (Quiroga, Fernández, Golluscio, & Blanco, 2013). Relationships among physiological traits and biomass production of plants grown under drought stress versus unstressed conditions were investigated in *T. crinita* (Greco & Cavagnaro, 2002; Quiroga, Golluscio, Blanco, & Fernández, 2010; Quiroga et al., 2013). The drought treatments significantly reduced total leaf blade dry matter, total and green leaf area, culms + sheaths dry matter and total aerial biomass. Differential response to drought was found among the accessions evaluated, and such response was associated with the extent of aridity conditions at the seed collection site of the accessions.

Besides the different response to drought observed among *T. crinita* accessions, different water-use strategies have been detected in plants of this species. Plants from extremely arid sites were more tolerant to drought than plants from humid regions, as indicated by the lower rate of water consumption from the soil, less leaf senescence and greater cell elongation rate observed in the formers (Quiroga et al., 2013).

In summary, the accessions from the most arid collection site were the least affected under drought conditions, displaying comparably higher biomass production, higher leaf water potential and postponement of the visual signs of drought stress. This suggests an adaptive mechanism for *T. crinita* populations grown in extremely arid regions. The strong relationship found between the aridity conditions at the seed collection site, the plant morphology, and the degree of tolerance to drought stress, suggests that collecting seed in extremely arid regions may be an effective strategy for further increasing drought tolerance in *T. crinita* germplasm.

5 | GENETIC DIVERSITY—EVIDENCE FROM MOLECULAR AND MORPHOLOGICAL DATA

5.1 | Morphological data

Broad and significant variation for morphometric and morphological traits, including aerial biomass production (described above), has been reported in natural populations of the species (Gil Báez et al., 2015) and in a genetically diverse collection of 20 *T. crinita* accessions (Cavagnaro et al., 2006). Table 2 presents the extent of morphological variation found in this collection. In general, the coefficient of variation (CV) for the quantitative traits (e.g., dry matter, culm height, basal diameter) in each accession was <0.20, whereas discrete morphological characters (e.g., colour of spike, growth habit, presence/absence of aerial tillers) were fixed in each accession. For most traits, the variation found among the accessions was consistent across three locations and three years, suggesting a

TABLE 2 Morphological and quantitative agronomic characters of 20 *Trichloris crinita* accessions

Accession No.	Dry matter (g/plant)	Culm height(cm)	Foliage height (cm)	Basal diameter(cm)	Culm number	TLB[a]	TLS[a]	TELS[b]	Colour of spike[c]	Colour internode[c]	Colour of node[c]	Colour of ligule[c]	Aerial tillers[b]	Growth habit[d]	Blade width (mm)	Blade length (mm)
1	88.1	78.1	16.4	12.4	52.4	−	+	−	R	R	R	R	+	SD	**5**	101
2	61.2	71.8	17.8	13.5	40.8	−	−	−	R	G	R	R	+	D	3	75
3	118.5	85.6	21.1	14.0	52.7	−	−	+	R	G	R	R	+	D	3.5	86
4	48.0	71.6	13.2	11.7	34.0	−	−	−	G	G	G	G	−	D	2.5	85
5	33.3**	53.4**	10.2**	9.1**	13.9**	+++	+++	+	G	G	R	R	+	SU	4.5	120
6	161.5	**95.1**	25.8	14.6	53.4	−	+++	+	R	G	R	R	+	SU	**5**	165
7	53.5	75.4	18.6	12.1	33.9	++	++	+	R	G	G	R	+	SU	**5**	**175**
8	74.9*	81.4*	18.6*	12.6*	25.2*	++	++	+	G	G	R	R	+	D	**5**	140
9	41.5	74.4	14.7	12.6	34.3	−	−	−	G	G	R	R	−	D	2	83
10	123.7	95.1	23.2	13.3	65.0	−	−	+	G	G	R	R	+	SD	**5**	144
11	**189.5**	91.8	**28.6**	**16.1**	**71.2**	−	++	+	R	G	R	R	+	SU	**5**	103
12	62.8**	52.4**	9.3**	9.2**	29.5**	++	++++	+	G	G	G	R	−	SU	3	93
13	88.2	85.0	21.9	11.4	65.3	−	−	+	R	R	R	R	+	U	4	95
14	22.3	63.6	12.4	10.3	46.1	−	++	−	G	G	G	G	−	SD	2.5	80
15	106.7	92.2	19.3	13.0	38.2	−	−	+	G	G	R	R	+	SU	4	110
16	169.3	84.3	27.4	14.5	53.7	−	−	+	G	G	R	R	+	SD	4	110
17	103.2*	91.5*	22.5*	13.2*	52.3*	−	−	+	G	G	R	R	+	SD	4.5	168
18	88.5	85.3	22.4	13.4	39.2	−	−	+	G	G	R	R	+	SU	4	140
19	142.1	82.2	27.1	14.9	64.6	−	−	+	G	G	R	R	+	SU	5	127
20	134.7	87.1	22.0	14.5	59.5	++	−	na	G	G	G	na	na	SU	4	na

na, not available; TLB, trichomes on the leaf blade; TLS, trichomes on the leaf sheath; TELS, trichomes on the edge of the leaf sheath.

Ten plants per accession were grown in three locations (30 plants/accession in total) and evaluated during 3 years. Data from the variables dry matter, culm height, foliage height, basal diameter and culm number are mean values from three years and three locations. Exceptions are indicated for means calculated from three years/two locations (*) and three years/one location (**).

Bold and italic numbers indicate the upper and lower extremes, respectively, of each quantitative character. Table from Cavagnaro et al. (2006).

[a](−) absent; (+) very scarce; (++) scarce; (+++) medium density; (++++) highly dense.

[b](−) absent; (+) present.

[c]R, red; G, green.

[d]D, decumbent; SD, semi-decumbent; SU, semi-upright; U, upright.

strong genetic basis for the observed morphological differences. Interestingly, significant positive correlations between biomass production and seven morphological and quantitative characters were found. Of these, culm height, foliage height, basal diameter and number of culms/plant were associated with biomass production at "r" values higher than 0.70. Accessions with high biomass tend to have plants with tall foliage and a large number of long culms holding leaves with broad blades. Also, a large basal diameter and the presence of aerial tillers and of trichomes on the edge of the leaf sheath were usually associated with productive phenotypes. Plant height and basal diameter were strongly correlated (0.89 and 0.83, respectively) with biomass production.

In a more recent study, Gil Báez et al. (2015) reported broad variation in morphological characters among *T. crinita* populations, as well as positive correlations between biomass production and the morphological characters mentioned above, in agreement with previous results by Cavagnaro et al. (2006). These traits may serve as morphological markers to aid in the selection of *T. crinita* plants with high biomass yield.

5.2 | Molecular data

Genetic diversity was assessed in the *T. crinita* collection of GBNG-IADIZA mentioned above using AFLP markers (Cavagnaro et al., 2006). For this purpose, a total of 1855 AFLP amplicons were analysed, of which 930 (50.1%) were polymorphic in at least two accessions. The analysis allowed the discrimination of all *T. crinita* accessions, and revealed broad genetic diversity in the GBNG-IADIZA collection, as indicated by the accessions pairwise genetic similarity (GS) values, which ranged from 0.31 to 0.92 with a mean of 0.57 (Jaccard coefficient).

5.3 | Molecular markers associated with biomass production

Biomass yield is one of the most important traits in plant species used as forage, and the identification of productive genotypes is crucial when aiming at increasing forage biomass, e.g., in a breeding programme. The study of Cavagnaro et al. (2006) revealed 18 AFLP markers significantly associated ($p \leq .05$) with biomass production (i.e., for these markers, "presence of a band" was exclusively or predominantly observed in highly productive genotypes, whereas the band was absent in genotypes with medium and low biomass). Of these, eight markers were completely correlated ($r = 1.00$) with biomass production, while the remaining 10 markers were partially associated with the trait ($r = .75$–.87). These markers can be used to assist selection for high forage production. Moreover, their usefulness would be greatly enhanced if they could be cloned and the sequence used to develop more robust and less labour-intensive PCR-based markers (Paran & Michelmore, 1993).

5.4 | Molecular resources in Trichloris

Trichloris molecular resources are very scarce. The study of Cavagnaro et al. (2006) represents the first and only report in which molecular markers were used in this genus. Despite the large number of AFLPs that were evaluated in that study, more robust and informative PCR-based markers, such as microsatellites or simple sequence repeats (SSRs), are desirable—and are lacking to date—in *Trichloris*. SSRs are generally favoured over AFLPs due to their high level of polymorphism, codominant inheritance and reproducibility. However, sequence data are needed to develop SSR markers, whereas AFLPs require no sequence information.

Very few DNA sequences of *Trichloris* are available at the National Center for Biotechnology Information (NCBI) and other GenBank databases, and the available sequences correspond to chloroplast and ribosomal DNA genes used for phylogenetic analysis. Although to date only 34 nucleotide sequences of *Trichloris* are available at NCBI, sequence data for the related genera *Chloris* and *Cynodon* are more abundant and include both DNA and mRNA (EST) sequence. Such data, from these and other *Trichloris*-related taxa, can be exploited to increase molecular resources in *Trichloris*. For example, using bioinformatic software, SSRs can be identified in sequence from *Chloris* and *Cynodon*, and primers flanking the SSR can be designed and evaluated in *Trichloris*. This approach has been successfully used to develop SSR markers in various species for which sequence data are lacking, with high marker transferability generally observed among closely related taxa (Cavagnaro et al., 2011; Peakall, Gilmore, Keys, Morgante, & Rafalski, 1998).

In conclusion, substantial genetic variation was found among *T. crinita* accessions, especially considering that the study of Cavagnaro et al. (2006) included only accessions that derived from arid and semi-arid regions of Argentina, and therefore, broader genetic diversity can likely be found in *T. crinita* natural populations from other regions/countries. The broad genetic diversity observed in *T. crinita* germplasm at the DNA level is consistent with the extensive phenotypic diversity reported in various studies for numerous traits, including biomass production, forage quality, morphological, physiological and phenological traits, and tolerance to abiotic stresses. The eventual use of molecular markers for tagging genes and specific alleles controlling these traits (e.g., by linkage mapping) will facilitate and accelerate the selection of plants—from natural populations or germplasm collections—with superior phenotypes for these traits. Thus, the huge intraspecific genetic variation for traits of importance for forage and revegetation purposes, the incipient development of molecular tools and the recent knowledge on the sexual reproductive behaviour of *T. crinita* encourage the development of breeding programmes in this species.

TABLE 3 Seed germination studies in *Trichloris crinita*

Origin of *T. crinita* population	Treatment	Germination percentage (%)	References
Argentina	15°C for 30 h and 25°C for 9 h	98	Cabeza, Brevedad, Fioretti, and Laborde (1999)
Argentina	30°C	99	Marone, Horno, and González Solar Del (2000)
Mexico	27°C for 10 h and 33°C for 14 h	80	Pezzani and Montaña (2006)
Argentina	25–30°C	90	Di Giambatista et al. (2010)
Argentina	28–35°C	>80	Zabala et al. (2011)

6 | RESPONSE TO GRAZING—SIMULATED DEFOLIATION EFFECTS

Knowledge regarding plant response to the frequency, intensity and timing of defoliation is necessary for developing successful grazing strategies. Defoliation affects many physiological processes. Reduction in leaf area and the period of photosynthetic inactivity are linked to intensity and frequency of defoliation.

Simulation studies showed that *Trichloris crinita* is tolerant to frequent defoliation but not to intense defoliation (intense defoliation was simulated by cuttings at ground level and up to five cm) (Cavagnaro & Dalmasso, 1983). Dry-matter yield was highest at 15 cm cutting height. More frequent or intense cutting (i.e., cutting at ≤5 cm from ground level) affects the reseeding capacity because the plants are not able to flower (Cavagnaro & Dalmasso, 1983). Detrimental effects of intense defoliation are due to the fact that basal buds are located in the crown of the plant, and therefore, intense grazing can negatively affect the production of new tillers.

It must be noted that the study of Cavagnaro and Dalmasso (1983) was conducted using *T. crinita* plants that had the predominant morphotype found in natural populations of this species (i.e., plants with upright growth habit) and excluded plants with prostrate architecture (<15 cm tall). Thus, although their results derived from simulations on plants with upright grow habit, the authors stated that prostrate accessions (e.g., accessions 4, 12 and 15 in Table 2) would also be suitable for cattle grazing, as long as cutting heights are kept above 5 cm from the ground.

Interestingly, Quiroga et al. (2010) found that *T. crinita* plants derived from seeds collected in heavily graced sites exhibited lower forage digestibility (due to higher lignin and cellulose content) than plants from ungraced or lightly graced sites, suggesting an adaptive grazing-avoidance mechanism associated to the intensity of grazing in the seed collection sites. Further research is needed to estimate the practical implications of these results in the management of this species as forage.

7 | SEED GERMINATION

Seed germination is critical for the establishment of seedlings (Harper, 1977). Factors affecting the germination of seeds determine the success of programmes for domestication of wild species (Casler & van Santen, 2010) and the sowing strategies for restoration

(Bischoff, Vonlanthen, & Steinger, 2006), and constitute an important aspect in the conservation and maintenance of germplasm banks. Different temperature treatments have been used to evaluate seed germination in *T. crinita* populations from different origins (Table 3). In general, high germination rates are achieved when *T. crinita* seeds are sown under relatively warm temperatures, in most cases above 25°C. Despite the higher germination rate observed at relatively high temperatures (>25°C), *T. crinita* seeds can germinate under a wide range of temperatures (15–40°C) (Greco, Cavagnaro, & Marone, 2003), increasing seedling competitiveness, as suggested by Zabala, Widenhorn, and Pensiero (2011).

Germination traits in many species present large differences among the seed provenances (Bischoff et al., 2006). The use of local seed sources is often recommended in restoration because they are thought to be better adapted to local habitat conditions, and the use of non-local seed might involve environmental risks, such as invasions of more aggressive genotypes (Saltonstall, 2002) and unwanted hybridization, particularly outbreeding depression (Byrne, Stone, & Millar, 2011; McKay, Christian, Harrison, & Rice, 2005).

However, these restoration guidelines often assume that the species used for revegetation are cross-pollinated and woody. Therefore, such recommendations may not always be suitable, or represent the best available strategy, for revegetation with predominantly self-pollinated species with short life cycles (i.e., annual or biennial plants), such as most of the Australian native grasses (Whalley et al., 2013) and *Trichloris crinita* (Kozub et al., 2017). According to Razanajatovo et al. (2016), plants with selfing ability and short life cycle are more likely to establish outside their historical range because they can reproduce from a single individual when mates or pollinators are not available. This suggests that, in the case of self-pollinated grasses, revegetation of degraded land can be successfully achieved using introduced seed, as long as the environment conditions at the seed collection site are similar to the environment of the revegetation site.

According to Whalley et al. (2013), using local provenance is most important where a complex outcome is the goal and the starting environment has undergone little modification (e.g., when restoring a grassland with a particular species that has become impoverished or extinct, or when trying to save rare and endangered native grasses). In these cases, the species involved are generally less studied and the genetic risks associated with the use of non-local seed are perhaps higher (Whalley et al., 2013). Conversely, in large-

scale revegetation projects where the environment has been severely modified (e.g., in a mine site or after a highway construction), the risks of undesirable genetic effects using non-local seed are relatively small. Furthermore, under these extreme land-degradation conditions, the use of introduced seed from species with well-understood breeding systems and commercial availability of large quantities of seed with certified quality (purity and viability) is usually advised over less studied local seed sources (Whalley et al., 2013).

In general, the performance of an accession or species at particular sites may be predicted by comparing the environments of the sites in which they were collected with those of the sites in which they are going to be sown (Whalley et al., 2013). Thus, the *Trichloris crinita* accessions at the GBNG-IADIZA, which were collected from diverse environments in the extensive phytogeographical region of Monte (Argentina), may likely be useful for revegetation purposes not only in Argentina, but also in similar arid and semi-arid regions of the world.

Another factor to consider is seed weight. In general, when germination conditions are optimal, the correlation between seed weight and germination percentage is not evident (Wang, Baskin, Cui, & Du, 2009), but under suboptimal conditions, the germination of *T. crinita* was positively correlated with seed weight (Zabala et al., 2011). Presumably, under stress conditions larger seeds have greater capacity to mobilize metabolic resources over a longer period during the germination and seedling growth (Kidson & Westoby, 2000). This suggests that *T. crinita* accessions with high yield of seeds set, and particularly of large seeds, are more suitable for their utilization in extreme environments.

An important problem for seed production is the presence of awns which difficult the harvest and seeding of *T. crinita* seeds. Recently, a harvest machine was developed at the Instituto Nacional de Tecnología Agropecuaria (INTA) in Argentina (Mora, 2014), and a threshing machine in currently being developed in the same institution (Mora, personal communication).

8 | RESTORATION AND REHABILITATION OF DEGRADED AREAS

Frequent rehabilitation strategies are as follows: sowing forage species (Blanco, Ferrando, Biurrun, Orionte, & Namur, 2005; Passera, Borsetto, Candia, & Stasi, 1992), treatments to improve soil quality (Prober, Thiele, Lunt, & Koen, 2005), or creating favourable microsites for establishment and growth of plants (Doust, Erskine, & Lamb, 2006; Passera et al., 1992; Zuleta, Li Puma, & Bustamante Leiva, 2003).

Passera et al. (1992) reported for an arid site in Argentina, which was maintained ungrazed during 20 years, that, after shrub removal the litter material that remained on top of the soil promoted the soil cover of forage species, including *T. crinita*. Conversely, seed addition did not improve forage cover, suggesting the existence of substantial natural seed bank of these native grasses in the exclosures.

Trichloris crinita had a good response, behaving as "pioneer species" (i.e., species capable of quick establishment), covering areas where shrubs were removed, and significantly increasing the overall forage coverage and livestock grazing capacity. Thus, competition of shrubs seemed to be a more important limiting factor than seed availability in ungrazed areas. Unlike ungrazed areas, in overgrazed rangelands of arid regions, the only rehabilitation strategy which increased the density of forage grasses was seed addition (Quiroga, Blanco, & Orionte, 2009). In these cases, competition with shrubs is less important compared to other factors, such as soil compaction, lack of seeds and litter cover (Suding, Gross, & Houseman, 2004). These results suggest that in order to define the rehabilitation strategy it is necessary to evaluate the natural seed bank and determine whether the area was overgrazed or not.

In arid regions, natural vegetation is commonly arranged in patches (Aguiar & Sala, 1999) and some plants can benefit from growing close to others, as this vicinity can ameliorate extreme microenvironmental conditions, improve resource availability or protect against herbivory. This positive interaction is known as "facilitation" and has implications in restoration of degraded areas. The application of facilitation strategies in restoration projects may improve the establishment of target plants, simulating a natural process (Padilla & Pugnaire, 2006).

Cavagnaro and Trione (2007) studied the possibility of using *T. crinita* in revegetation programmes of arid regions under tree–grass association systems. Physiological, morphological and biochemical parameters were assessed under different levels of shade. Under shade, *T. crinita* plants revealed significantly reduced growth compared to controls under full sunlight. The number of total tillers decreased with increased shade. The reduction in growth due to shade did not affect dry-matter partitioning. The typical upright growth habit of *T. crinita* observed under full sunlight was gradually modified under shade regimes, exhibiting a tendency to a prostrate growth as shading increased. Shading treatments had no effect on the following biochemical parameters: nitrogen concentration, total non-structural carbohydrates, protein content in crown, forage quality and nitrogen use efficiency. Interestingly, under the most extreme shading regime *T. crinita* plants maintained positive dry-matter accumulation (Cavagnaro & Trione, 2007).

Thus, it is possible to use *T. crinita* in revegetation programmes under tree–grass association as observed under *Prosopis* canopies in many areas of Monte in Argentina (Greco, Sartor, & Villagra, 2013).

9 | DEVELOPING LOCALLY ADAPTED *T. CRINITA* CULTIVARS FOR GRAZING AND REVEGETATION IN DEGRADED DRY LANDS

A vast proportion of the world's dry lands present some extent of land degradation, the direct consequences of which include increased rates of erosion, loss of biodiversity, and reduced soil fertility and productivity (Bedunah & Angerer, 2012). Diverse strategies used to recover such degraded ecosystems were not always

successful. Initial attempts to restore degraded lands did not consider the underlying ecological processes (Call & Roundy, 1991). Restoration programmes were based on reseeding degraded areas with introduced grasses due to the perception that these species were more readily established, more productive, and more persistent (Waters & Shaw, 2003). However, with the exception of *Cenchrus* spp. (i.e., buffelgrass), all introduced grass species failed to persist in areas of low and highly variable rainfall (Johnston, 1990), as indicated from previous experiences in the state of Queensland, Australia, and Texas and Arizona, in United States (Marshall, Lewis, & Ostendorf, 2012; Waters & Shaw, 2003).

In the last decades, numerous studies have reported that native grass species are more suitable than introduced species for restoration projects in arid and semi-arid regions (Waters & Shaw, 2003). In addition to adaptive advantages, native species have, in general, lower requirements in terms of nutrients and establishment costs (Wilson, 1996). Moreover, some native species are very resilient to climatic extremes, yet maintaining good productivity (Jefferson et al., 2002).

Knowledge on physiological, ecological and genetic aspects of native grasses is essential for selecting the most suitable species—and genotypes within a species—for each agroecological situation. In the case of *T. crinita*, locally adapted germplasm has been characterized for various traits including biomass production, protein content, seed yield, photoassimilates partitioning, tolerance to grazing and drought, and suitability for restoration of degraded areas. It is expected that cultivar development for meeting specific needs will be facilitated, either via sexual intercrossing or direct selection of genotypes with the desired combination of characteristics. To date, two *T. crinita* cultivars are registered in Argentina [Chamical INTA (n°13645) and San Juan-IAD (n°15155)] and at least three *T. crinita* cultivars, varying in biomass productivity, seed yield and degree of drought tolerance, are being registered and expected to be released soon in Argentina (Cavagnaro, personal communication). In United States, Kika de la Garza Plant Material Center developed a cultivar of *T. crinita* in 1999 named "Kinney germplasm" (Lloyd-Reilley & Kadin, 2002).

Successful examples of cultivar development for native grass species in other countries have been reported. For example, the United States Department of Agriculture's Natural Resources Conservation Service (USDA-NRCS) has developed cultivars (ecotypes) for all US major native grasses (Vogel & Pedersen, 1993), whereas more than 20 ecovarsTM (ECOlogical VARiety) have been developed from various native grasses, including blue grama (*Bouteloua gracilis*), in Western Canada (Smith & Whalley, 2002). In Australia, improved cultivars have been released since the 1980s for many native grass species, including *Austrodanthonia richardsonii* (cv Hume, cv Taranna), *Themeda triandra* (cv Tangara, cv LIG 520), *Microlaena stipoides* (cv Shannon, cv LIG 183), *Austrodanthonia bipartita* (cv Bunderra) (Cole & Johnston, 2006; Waters et al., 2000; Young & Crosthwaite, 2007).

10 | CONCLUSIONS AND FUTURE PROSPECTS

In the last decades, plant biologists have characterized the variation present in *T. crinita* germplasm for a number of genetic and physiological traits that are of interest for this forage species. Genetic diversity studies *via* morphological and molecular marker (AFLP) analysis, as well as evaluations of quantitative agronomic traits, such as forage biomass production, were performed. Plant physiological responses under normal (unstressed) and stressed conditions, such as drought or salinity, were investigated in various published reports, revealing interesting information not only from a physiological point of view, but also suggesting adaptive mechanisms underlying such traits in natural *T. crinita* populations. In addition, several studies focused on applied aspects regarding the use of this species for forage or restoration purposes, including analysis of forage nutritional quality, response to grazing, seed quality and viability, and the implementation of strategies for its use in restoration and rehabilitation of degraded areas. It is expected that the vast and diverse information generated throughout these studies, in basic and applied research, will enhance the use of *Trichloris crinita* for various purposes.

The characterization of the genetically diverse *T. crinita* germplasm collection at GBNG-IADIZA represents a foundational body of knowledge for the utilization of these materials. For example, different *T. crinita* accessions can be readily chosen based on several traits of interest and depending on the purpose of use. Also, morphological traits strongly correlated with biomass production can be used to select plants with high biomass yield in natural *T. crinita* populations, as these traits are easy to visualize and score. The available molecular markers completely associated with high biomass content can be used later in the laboratory to confirm field selections, especially if these AFLP markers are converted to more robust PCR-based markers, such as SCARs (sequence characterized amplified regions). Registration of these materials would facilitate the legal protection of *T. crinita* varieties, and the production and distribution of seeds with certified genetic identity and quality.

Very recently, the mode of reproduction of *T. crinita* was elucidated. These data, together with knowledge on the floral phenology, will facilitate the design of pollination experiments aimed at intercrossing selected genotypes for developing populations that segregate for traits of interest. This would allow a number of genetic studies, including inheritance analyses, genetic and QTL mapping, and the development of markers tightly linked to desirable traits, useful for marker-assisted selection. The possibility of intercrossing *T. crinita* genotypes previously characterized based on relevant agronomic traits—such as biomass yield, nutritional quality, palatability and drought resistance—would facilitate breeding new varieties that combine specific traits of interest, suitable for their use as forage under different agroecological environments. With regard to its use as forage for feeding livestock, the selection of *T. crinita* accessions with trampling and grazing tolerance, good nutritional quality and high biomass production is now possible. Thus, important advances

in breeding, genetics and the development of molecular resources are expected for this species.

In revegetation and rehabilitation programmes, it is important that seed germination occurs under a broad range of temperatures. The possibility to choose genotypes resistant to drought for degraded areas, or genotypes with large partitioning of photoassimilates to roots, in order to control erosion and stabilize subsoil, will have a positive impact in restoration projects. A strong relationship between site of origin and plant morphological characteristics provides evidence for local adaptation in *T. crinita*. Undoubtedly, these adaptations to different environmental conditions—particularly those related to soil characteristics, water availability, abiotic stresses such as drought and salinity, and competition with other native grasses—have shaped the broad genetic and phenotypic variation observed today in some germplasm collections of this species, such us the GBNG-IADIZA. Such variation can be exploited for restoration of degraded areas with similar environmental conditions as those in the seed collection sites of the accessions selected for revegetation. As learned from the experience of revegetation projects with Australian self-pollinated native grasses, the recommendation of matching the local environmental factors is, likely, of greater importance than using locally collected seed sources. The predominance of selfing in *Trichloris crinita* ensures that large numbers of locally fit individuals adapted to prevailing conditions are produced.

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CONFLICT OF INTEREST

The authors of this work declare no conflict of interest.

ORCID

P. F. Cavagnaro http://orcid.org/0000-0001-5838-0876

REFERENCES

Aguiar, M. R., & Sala, O. E. (1999). Patch structure, dynamics and implications for the functioning of arid ecosystems. *Trends in Ecology & Evolution*, 14, 273–277.

Anderson, D. E. (1974). Taxonomy of the genus Chloris. *Brigham Young University Science Bulletin. Biological Series*, 29, 1–133.

Anton, A., Zuloaga, F. O., & de Rúgolo Agrasar, Z. E. (2012). *Flora Argentina: Flora vascular de la República Argentina*. Córdoba, Argentina: Graficamente Ediciones.

ARC (1980). *The nutrient requirements of ruminant livestock* (351 pp). Farnham Royal, UK: Commonwealth Agric. Bureaux.

Barrett, S. C. H. (2003). Mating strategies in flowering plants: The outcrossing-selfing paradigm and beyond. *Philosophical Transactions of the Royal Society of London Series B*, 358, 991–1004.

Bedunah, D. J., & Angerer, J. P. (2012). Rangeland degradation, poverty, and conflict: How can rangeland scientists contribute to effective responses and solutions? *Rangeland Ecology & Management*, 65, 606–612.

Bischoff, A., Vonlanthen, B., & Steinger, T. (2006). Seed provenance matters-effects on germination of 4 plant species used in ecological restoration. *Basic and Applied Ecology*, 7, 347–359.

Bisht, M. S., & Mukai, Y. (2000). Mapping of rDNA on the chromosomes of *Eleusine* species by fluorescence in situ hybridization. *Genes & Genetic Systems*, 75, 343–348.

Blanco, L. I., Ferrando, C. A., Biurrun, F., Orionte, E. L., & Namur, P. (2005). Vegetation responses to roller chopping and buffelgrass seeding in Argentina. *Rangeland Ecology and Management*, 58, 219–224.

Brilman, L. A., Kneebone, W. R., & Endrizzi, J. E. (1982). Pachytene chromosome morphology of diploid *Cynodon dactylon* (L.) Pers. *Cytologia*, 47, 171–181.

Byrne, M., Stone, L., & Millar, M. A. (2011). Assessing genetic risk in revegetation. *Journal of Applied Ecology*, 48, 1365–1373.

Cabeza, C. E., Brevedad, R. E., Fioretti, M. N., & Laborde, H. E. (1999). The influence of dehulling and seed storage on the germination of the range grasses of the Caldenal (Argentina). *Seed Science & Technology*, 27, 359–363.

Cabrera, A. L. (1976). Regiones Fitogegráficas de Argentina. In A. L. Cabrera (Ed.), *Enciclopedia Argentina de Agricultura y Jardinería. Tomo II. Fascículo I* (pp. 1–85). Buenos Aires, Argentina: ACME.

Cabrera, A. L. (1994) Regiones Fitogegráficas de Argentina. In A. L. Cabrera (Ed.), *Enciclopedia Argentina de Agricultura y Jardinería. Tomo II. Fascículo I* (pp. 1–85). Buenos Aires, Argentina: ACME.

Call, C. A., & Roundy, B. A. (1991). Perspectives and processes in revegetation of arid and semiarid rangelands. *Journal of Range Management*, 44, 543–549.

Casler, M. D., & van Santen, E. (2010). Breeding Objectives in Forages. In B. Boller, U. K. Posselt & F. Veronesi (Eds.), *Handbook of plant breeding. Fodder Crops and Amenity Grasses* (pp. 115–136). New York, NY: Springer.

Cavagnaro, J. B. (1988). Distribution of C3 and C4 grasses at different altitudes in a temperate arid region of Argentina. *Oecologia*, 76, 273–277.

Cavagnaro, P. F., Cavagnaro, J. B., Lemes, J. L., Masuelli, R. W., & Passera, C. B. (2006). Genetic diversity among varieties of the native forage grass *Trichloris crinita* based on AFLP markers, morphological characters, and quantitative agronomic traits. *Genome*, 49, 906–918.

Cavagnaro, P. F., Chung, S. M., Manin, S., Yildiz, M., Ali, A., Alessandro, M. S., . . . Simon, P. W. (2011). Microsatellite isolation and marker development in carrot - genomic distribution, linkage mapping, genetic diversity analysis and marker transferability across Apiaceae. *BMC Genomics*, 12, 386.

Cavagnaro, J. B., & Dalmasso, A. (1983). Response to different intensity and frequency of cutting in native grasses of Mendoza *Pappophorum caespitosum* and *Trichloris crinita*. *Deserta*, 7, 203–218.

Cavagnaro, J. B., Dalmasso, A. D., & Candia, R. J. (1983). Distribución vertical de materia seca en gramíneas perennes de la llanura oriental de Mendoza. *Deserta*, 7, 271–289.

Cavagnaro, J. B., & Trione, S. O. (2007). Physiological, morphological and biochemical responses to shade of *Trichloris crinita*, a forage grass from the arid zone of Argentina. *Journal of Arid Environments*, 68, 337–347.

Cerqueira, E. D., Sáenz, A. M., & Rabotnikof, C. M. (2004). Seasonal nutritive value of native grasses of Argentine Calden Forest Range. *Journal of Arid Environments*, 59, 645–656.

Chirino, C. C., Grahn, K. N., & Robles, L. E. (1988). Determinación de proteína bruta de algunas especies forrajeras de La Pampa. *Revista de la Facultad de Agronomía UNLPam*, 3, 57–74.

Clayton, W. D. (1967). Studies in the Gramineae: XIII. Chlorideae. *Kew Bulletin*, 21, 99–110.

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KOZUB ET AL.

Cole, I. A., & Johnston, W. H. (2006). Seed production of Australian native grass cultivars: An overview of current information and future research needs. *Animal Production Science*, 46, 361–373.

Díaz, H. B., Lagomarsino, E. D., Prete, I. R., & Rodríguez J.C, R. E. Y. . (1970). Productividad de las pasturas naturales de las zonas ganaderas de Tucumán. *Revista de Agronomía Noroeste Argentino*, 7, 675–724.

Dickerson, J., & Wark, B. (1997). Vegetating with native grasses in northeastern North America. Ducks Unlimited Canada. In E. Grossbard & D. Atkinson (Eds.), *The herbicide glyphosate* (490 pp). Boston, MA: Butterworths & Co.

Doust, S. J., Erskine, P. D., & Lamb, D. (2006). Direct seeding to restore rainforest species: Microsite effects on the early establishment and growth of rainforest tree seedlings on degraded land in the wet tropics of Australia. *Forest Ecology and Management*, 234, 333–343.

Duncan, T. M., & Rausher, M. D. (2013). Evolution of the selfing syndrome in Ipomoea. *Frontiers in Plant Science*, 4, 1–8.

Fedorov, A. A. (1969). *Chromosome number of flowering plants* (926 pp). Leningrad: Published by Komarov Botanical Institute U.S.S.R. National Academy of Sciences.

Gabutti, E. G., Cozzarín, I. G., Reynoso, M., Privitello, M. J. L., Pensiero, J., & Zabala, J. M. (2011). Caracterización agronómica de poblaciones nativas de *Trichoris crinita* y *T. pluriflora*. *Revista Argentina de Producción Animal*, 31, 574.

Di Giambatista, G., Garbero, M., Ruiz, M., & Pedranzani, A. G. H. (2010). Germination of *Trichloris crinita* and *Digitaria eriantha* under abiotic stress conditions. *Pastos y Forrajes*, 33, 1–10.

Gil Báez, C., Ordinola Agüero, R., Ernst, R. D., & Ruiz, M. A. (2015). Caracterización morfológica, biomasa aérea y calidad en distintas poblaciones de *Trichloris crinita*. *Archivos de Zootecnia*, 64, 49–56.

GLP, Global Land Project (2005). Science Plan and Implementation Strategy" [IGBP (International Geosphere Biosphere Program)Report No. 53/International Human Dimensions Programme Report No. 19, IGBP Secretariat, Stockholm, 2005]; www.globallandproject.org/documents.shtml

Greco, S. A. (1996). *Algunas causas ecofisiológicas de variaciones intraespecíficas en productividad de Trichloris crinita (Lag. Parodi) (pasto de hoja)*. Buenos Aires, Argentina: Universidad de Buenos Aires.

Greco, S. A., & Cavagnaro, J. B. (2002). Effects of drought in biomass production and allocation in three varieties of *Trichloris crinita* P. (Poaceae) a forage grass from the arid Monte region of Argentina. *Plant Ecology*, 164, 125–136.

Greco, S. A., & Cavagnaro, J. B. (2005). Growth characteristics associated with biomass production in three varieties of *Trichloris crinita* (Poaceae), a forage grass native to the arid regions of Argentina. *The Rangeland Journal*, 27, 135–142.

Greco, S. A., Cavagnaro, J. B., & Marone, L. (2003). Temperature effects on seed germination of four forage grasses from Monte region, Argentina. *Boletin Sociedad Argentina de Botánica*, 38, 182.

Greco, S. A., Sartor, C. E., & Villagra, P. E. (2013). Minimum water input event for seedling emergence of three native perennial grasses of the Central Monte desert (Argentina) influenced by the effect of shade and the season of the year. *Revista de la Facultad de Ciencias Agrarias*, 45, 97–209.

Gupta, A., Sood, S., Agrawal, P. K., & Bhatt, J. C. (2012). Floral biology and pollination system in small millets. *The European Journal of Plant Science and Biotechnology*, 6, 80–86.

Gutiérrez, H. F., Richard, G. A., & Cerino, M. C. (2016). Sistema Reproductivo de *Trichloris* (Poaceae, Chloridoideae, Chlorideae). *Boletín de la Sociedad Argentina de Botánica*, 51, 111–122.

Harper, J. L. (1977). *Population biology of plants*. London, UK: Academic press.

Harris, R. B. (2010). Rangeland degradation on the Qinghai-Tibetan plateau: A review of the evidence of its magnitude and causes. *Journal of Arid Environments*, 74, 1–12.

Hilu, K. W., & Alice, L. A. (2001). A phylogeny of Chloridoideae (Poaceae) based on *matK* sequences. *Systematic Botany*, 26, 386–405.

Hitchcock, A. S. (1971). *Manual of the grasses of the United States (Vol. 2)*. New York, USA: Dover Publications Inc.

Jefferson, P. G., McCaughey, W. P., May, K., Woosaree, J., McFarlane, L., & Wright, S. M. B. (2002). Performance of American native grass cultivars in the Canadian prairie provinces. *Native Plants Journal*, 3, 24–33.

Johnston, P. W. (1990). Producing native seed for mulga lands. In P. M. Dowling, & D. L. Garden (Eds.), *Native grass workshop proceedings* (161 pp). Dubbo, NSW: Australian Wool Corporation Melbourne.

Khagram, S., Clark, W. C., & Raad, D. F. (2003). From the environment and human security to sustainable security and development. *Journal of Human Development*, 4, 289–314.

Kidson, R., & Westoby, M. (2000). Seed mass and seedling dimensions in relation to seedling establishment. *Oecologia*, 125, 11–17.

Kozub, P. C., Barboza, K., Galdeano, F., Quarin, C., Cavagnaro, J. B., & Cavagnaro, P. F. (2017). Reproductive biology of the native forage grass *Trichloris crinita* (Poaceae, Chloridoideae). *Plant Biology*, 19, 444–453.

Lemes, J. L. (1992). Metodología en la exploración del recurso fitogenético de forrajeras nativas. *Xerophytia*, 3, 1–21.

Lloyd-Reilley, J., & Kadin, E. (2002). *False rhodes grass, Chloris crinita* Lag. Plant Fact Sheet. Kingsville, Texas, USA: USDA, NRCS, Kika de la Garza Plant Material Center.

Lund, H. G. (2007). Accounting for the world's rangelands. *Rangelands*, 29, 3–10.

Marinoni, L., Bortoluzzi, A., Parra-Quijano, M., Zabala, J. M., & Pensiero, J. F. (2015). Evaluation and improvement of the ecogeographical representativeness of a collection of the genus *Trichloris* in Argentina. *Genetic Resources and Crop Evolution*, 62, 593–604.

Marone, L., Horno, M. E., & González Solar Del, R. (2000). Post-dispersal fate of seeds in the Monte desert of Argentina : Patterns of germination in successive wet and dry years. *Journal of Ecology*, 88, 940–949.

Marshall, V. M., Lewis, M. M., & Ostendorf, B. (2012). Buffel grass (*Cenchrus ciliaris*) as an invader and threat to biodiversity in arid environments: A review. *Journal of Arid Environments*, 78, 1–12.

May, K. W., Wark, B., & Coulman, B. (1997) Ecovar development on the northern great plains of North America. In: Proceedings of the XVII International Grasslands Congress, Winnipeg, Man., and Sas katoon, Sask. Section 1.89–1.90. Association Management Centre, Calgary, Alta.

McKay, J. K., Christian, C. E., Harrison, S., & Rice, K. J. (2005). How local is local? – A review of practical and conceptual issues in the genetics of restoration. *Restoration Ecology*, 13, 432–440.

MEA, Millennium Ecosystem Assessment (2005). *Ecosystems and human well-being: Desertification synthesis*. Washington, DC: World Resources Institute.

Mora, S. (2014). Hay avances en la cosecha de semilla de pasto plumerito. *Revista campo Andino*, 24, 28–29.

Namur, P. R., Blanco, L. J., Sancho, A. R. (2011). Respuesta forrajera de *Trichloris crinita* a la disponibilidad hídrica. *Revista Argentina de Producción Animal*, 31, 540.

Nicora, E. G., & de Rúgolo Agrasar, Z. E. (1987). *Los géneros de gramíneas de América austral* (611 pp). Buenos Aires, Argentina: Editorial Hemisferio Sur.

Padilla, F. M., & Pugnaire, F. I. (2006). The role of nurse plants in the restoration of degraded environments. *Frontiers in Ecology and the Environment*, 4, 196–202.

Papanastasis, V. P. (2009). Restoration of degraded grazing lands through grazing management: Can it work? *Restoration Ecology*, 17, 441–445.

Paran, I., & Michelmore, R. W. (1993). Development of reliable PCR-based markers linked to downy mildew resistance genes in lettuce. *Theoretical and Applied Genetics*, 86, 1033–1037.

Passera, C. B., Borsetto, O., Candia, R. J., & Stasi, C. R. (1992). Shrub control and seedling influences on grazing capacity in Argentina. *Journal of Range Management*, 45, 480–482.

Peakall, R., Gilmore, S., Keys, W., Morgante, M., & Rafalski, A. (1998). Cross species amplification of soybean (*Glycine max*) simple sequence repeats (SSRs) within the genus and other legume genera: Implications for the transferability of SSRs in plants. *Molecular Biology and Evolution*, 15, 1275–1287.

Peterson, P. M., Columbus, J. T., & Pennington, S. J. (2007). Classification and biogeography of new world grasses: Chloridoideae. *Aliso: A Journal of Systematic and Evolutionary Botany*, 23, 580–594.

Peterson, P. M., Romaschenko, K., Arrieta, Y.H. (2015). A molecular phylogeny and classification of the Eleusininae with a new genus, Micrachne (Poaceae: Chloridoideae: Cynodonteae). *Taxon*, 64, 445–467.

Peterson, P. M., Romaschenko, K., Snow, N., Johnson, G. (2012) A molecular phylogeny and classification of *Leptochloa* (Poaceae: Chloridoideae: Chlorideae) *sensu lato* and related genera. *Annals of Botany*, 109, 1317–1329.

Pezzani, F., & Montaña, C. (2006). Inter- and intraspecific variation in the germination response to light quality and scarification in grasses growing in two-phase mosaics of the Chihuahuan Desert. *Annals of Botany*, 97, 1063–1071.

Prober, S. M., Thiele, K. R., Lunt, I. D., & Koen, T. B. (2005). Restoring ecological function in temperate grassy woodlands: Manipulating soil nutrients, exotic annuals and native perennial grasses through carbon supplements and spring burns. *Journal of Applied Ecology*, 42, 1073–1085.

Quiroga, R. E. (2011). Variación morfológica en once poblaciones del pasto nativo *Trichloris crinita*. INTA EEA, Catamarca. Argentina. *Revista Argentina de Producción Animal*, 31, 539.

Quiroga, E., Blanco, L., & Orionte, E. (2009). Evaluación de estrategias de rehabilitación de pastizales áridos. *Ecología Austral*, 19, 107–117.

Quiroga, R. E., Fernández, R. J., Golluscio, R. A., & Blanco, L. J. (2013). Differential water-use strategies and drought resistance in *Trichloris crinita* plants from contrasting aridity origins. *Plant Ecology*, 214, 1027–1035.

Quiroga, R. E., Golluscio, R. A., Blanco, L. J., & Fernández, R. J. (2010). Aridity and grazing as convergent selective forces: An experiment with an Arid Chaco bunchgrass. *Ecological Applications*, 20, 1876–1889.

Razanajatovo, M., Maurel, N., Dawson, W., Essl, F., Kreft, H., Pergl, J., ... van Kleunen, M. (2016). Plants capable of selfing are more likely to become naturalized. *Nature Communications*, 7, 13313.

Saltonstall, K. (2002). Cryptic invasion by a non-native genotype of the common reed, *Phragmites australis* into North America. *Proceedings of the National Academy of Sciences of the United States of America*, 99, 2445–2449.

Seligman, N. G., Cavagnaro, J. B., & Horno, M. E. (1992). Simulation of defoliation effects on primary production of a warm-season, semiarid perennial-species grassland. *Ecological Modelling*, 60, 41–61.

Silva Colomer, J., Cavagnaro, J. B., Lemes, J., & Medero, M. (1989) Productivity and nutritive values in three ecotypes of *Trichloris crinita*, a native forage grass of the arid zones of Argentina. Proceedings of the XVI International Grassland Congress,1989, pp. 815–816. Montpellier, France.

Smith, S. R., & Whalley, R. D. B. (2002). A model for expanded use of native grasses. *Native Plants Journal*, 3, 38–49.

Suding, K. N., Gross, K. L., & Houseman, G. R. (2004). Alternative states and positive feedbacks in restoration ecology. *Trends in Ecology & Evolution*, 19, 46–53.

Vogel, K. P., & Pedersen, J. F. (1993). Breeding systems for cross-pollinated perennial grasses. *Plant Breeding Reviews*, 11, 251–274.

Wainstein, P., & Gonzalez, S. (1969). Valor nutritivo de plantas forrajeras del este de la provincia de Mendoza (reserva ecológica Ñacuñán). *Revista Facultad Ciencias Agrarias.*, 15, 133–142.

Wang, J. H., Baskin, C. C., Cui, X. L., & Du, G. Z. (2009). Effect of phylogeny, life history and habitat correlates on seed germination of 69 arid and semi-arid zone species from northwest China. *Evolutionary Ecology*, 23, 827–846.

Waters, C. M., & Shaw, N. L. (2003). Developing native grass seed industries for revegetation in Australia and the Western United States: a contrast in production and adoption. In: Proceedings of the VIIth International Rangelands Congress. Durban, South Africa.

Waters, C., Whalley, W., & Huxtable, C. (2000). *Grassed-up: Guidelines for revegetating with Australian native grasses*. Orange, NSW: NSW Agriculture.

Whalley, R. D. B., Chivers, I. H., & Waters, C. M. (2013). Revegetation with Australian native grasses – a reassessment of the importance of using local provenances. *The Rangeland Journal*, 35, 155–166.

Wilson, A. D. (1996). Native and low input grasses for pastoral and marginal cropping land. *New Zealand Journal of Agricultural Research*, 39, 465–469.

Young, A. G., & Crosthwaite, J. (2007). Genetic integrity as a target for natural capital restoration: Weighing the costs and benefits. In J. Aronson, S. J. Milton, & J. N. Blignaut (Eds.), *Restoring natural capital: Science, business, and practice* (pp. 85-93). Washington, DC: Island Press.

Zabala, J. M., Widenhorn, P., & Pensiero, J. F. (2011). Germination patterns of species of the genus *Trichloris* in arid and semiarid environment. *Seed Science & Technology*, 39, 338–353.

Zhang, J. Y., Wang, Y., Zhao, X., Xie, G., & Zhang, T. (2005). Grassland recovery by protection from grazing in a semi-arid sandy region of northern China. *New Zealand Journal of Agricultural Research*, 48, 277–284.

Zuleta, G. A., Li Puma, M. C., & Bustamante Leiva, A. (2003). Initial effects of branching designs to restore semiarid shrub steppes in abandoned oil and gas locations of Patagonia, Argentina. 15th Annual International Conference of the Society for Ecological Restoration, Austin, Texas, USA.