Revista Internacional de BOTANICA EXPERIMENTAL
ΦYTON
International Journal of EXPERIMENTAL BOTANY
Fundada en 1951 por Founded 1951 by
Miguel Raggio & Nora Moro-Raggio
Editor: Dr. Miguel Raggio
FUNDACION ROMULO RAGGIO
Gaspar Campos 861, 1638 Vicente López (BA), Argentina

49° ANIVERSARIO 69 (2000) 91-108 49th ANNIVERSARY

Phenology of some herbaceous and woody species in central, semiarid Argentina

(with 9 figures)

Giorgetti HD[1+], **Z Manuel**[2], **OA Montenegro**[1], **GD Rodríguez**[1], **CA Busso**[3,*]

Abstract. Phenolagical stages of several grasses, shrubs, trees and herbaceous dicots are described at a site typical of rangelands in the Monte Phytogeographical Province (Argentina). High soil water levels determined an extension of tillering during summer in the autumn-winter-spring perennial grasses, and during late-spring and summer in the spring-summer perennial grasses. This cautions about strictly classifying these grasses as either cool-or warm-season species. Stem elongation, flowering, fructification and/or seed dispersal in several perennial grasses, and the boot stage, flowering and/or the reproductive stage in some woody species occurred earlier in dryer than in wet springs. However, reproductive phenological phases in other perennial grass and woody species were either advanced or extended later into the season as years became wetter. During wet summers, sprouting can extend even until early autumn in the woody species. The temporal plasticity in the phenology of grasses, herbaceous dicots or woody species suggests they are well adapted to the great intra - and interannual variation in rainfall which can occur in the region under study.

Key words: phenology, semiarid Argentina, annual and perennial grasses, annual herbaceous dicots, shrubs and trees.

Resumen. Se describen los estadios fenológicos de especies de gramíneas, arbustos, árboles o dicotiledóneas herbáceas en un sitio típico de pastizales naturales en la Provincia Fitogeográfica del Monte. Altos niveles de agua en el

---

[1] Chacra Experimental de Patagones, Ministerio de Agricultura Ganadería y Alimentación de la Provincia de Buenos Aires, C.C.118, 8504-Carmen de Patagones, Provincia de Buenos Aires.

[2] Ministerio de Recursos Naturales, Provincia de Río Negro.

[3] Departamento de Agronomía-CERZOS, Universidad Nacional del Sur (UNSur), Consejo Nacional de Investigaciones Científicas y Técnicas (CONICET), Altos del Palihue, 8000-Bahía Blanca, Provincia de Buenos Aires,cebusso@criba.edu.ar

*To whom correspondence should be addressed

[+] Address for reprint request.

Financial support for this research was provided by the Ministerio de Agricultura Ganadería y Alimentación de la Provincia de Buenos Aires; CONICET and the Secretaría Gral. de Ciencia y Tecnología UNSur.

Received 21.XI.2000; accepted 28.XII.2000

suelo determinaron una extensión del macollaje durante el verano en las gramíneas perennes otoño-inverno-primaverales, y durante fines de primavera y verano en las gramíneas perennes estivales. Esto nos alerta en cuanto a clasificar estrictamente estas especies como otoño-inverno-primaverales o estivales. La elongación de tallos, floración, fructificación y/o dispersión de semillas en varias especies de gramíneas perennes, y los estadios de botón floral, floración y/o reproductivo en algunas especies leñosas ocurrieron antes en las primaveras secas que en las húmedas. Sin embargo, las fases fenológicas reproductivas en otras especies de gramíneas perennes y leñosas se adelantaron o extendieron hasta más tarde en la estación en años más húmedos. En veranos húmedos, el rebrote de leñosas puede extenderse aún hasta principios del otoño. La plasticidad temporal en la fenología de las gramíneas, dicotiledóneas herbáceas o leñosas sugiere que están bien adaptadas a la gran variación intra e interanual de la lluvia en la región estudiada.

Palabras clave: fenología, región semiárida de Argentina, gramíneas anuales y perennes, dicotiledóneas herbáceas anuales, arbustos y árboles.

Knowledge of when a plant will reach certain developmental stage can help in timing land management practices and in choosing the best time for sampling. Phenology, for e.g., is essential in determining the appropiate grazing time, minimizing negative herbivory effects on desirable components of rangeland vegetation (9). Comparative phenological development has received some attention in herbaceous and woody species in the Southern Caldenal, a phytogeographic region of about 40000 km^2 in central, semiarid Argentina (20, 13, 37, 14). However, these studies have provided only some general information on the phenology of these species or have been limited to a few species.

Rangelands in the Monte Phytogeographical Province, south of the Southern Caldenal, cover about 528000 km^2 in central Argentina and experience low and highly variable rainfall (long term range 100-400 mm per year) (41). Since precipitation can be a critical factor in phenology in arid and semiarid areas (5), species commonly found in these rangelands will have reproductive strategies that enable them to survive. It is also important to determine the extent of temporal plasticity in the phenology of species because it may contribute to explain their persistence in the community. This descriptive paper therefore focuses on providing a more detailed analysis or additional information of phenological events in several herbaceous and woody species at the Monte Phytogeographical Region.

MATERIALS & METHODS

Area description. The study was conducted at a site typical of rangelands at the Monte Phytogeographical Province, Province of Buenos Aires, Argentina. The study site (40° 39'S, 62° 54'W; 40 m a.s.l.) was 22 km away from Carmen de Patagones.

The climate, vegetation and soil characteristics of the region have been reported (11, 18, 41). The climate is temperate semiarid, mean annual temperature is 14.6 °C, and mean monthly temperatures of the coldest (July) and warmest (January) months vary from 3 to 12 °C and 19 to 27 °C, respectively; absolute minima and maxima vary from -5 to -17 °C and 35 to 46 °C. The mean relative humidity is 60%. Annual mean for winds is 13 km h^{-1}. Long-term average rainfall is 331 mm/year (28). Annual rainfall is concentrated during spring and fall. Air temperature, water vapor tension, and rainfall were measured by a meteorological station located at the study site (Fig. 1). Evapotranspiration was calculated (40); mean annual water deficit varied from 400 to 800 mm.

The community is characterized by an open shrubby stratum which includes herbaceous species of different grazing value. Cattle grazing on natural vegetation is the most important economic activity (11). In this paper annual or perennial grass and forb species of the herbaceous layer were categorized, on the basis of their acceptance by cattle, into desirable (highly preferred), intermediate (grazed when desirable species are not available) or undesirable (accepted only when better forage species are not available). Woody species were classified as evergreen or deciduous.

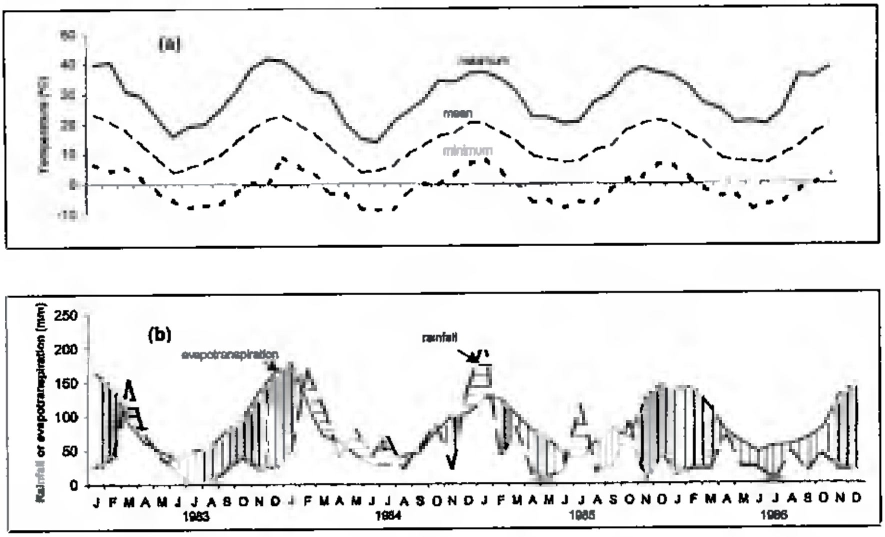

Fig. 1.– (a) Absolute monthly maxima and minima, and mean air temperatures, and (b) monthly rainfall and mean monthly evapotranspiration during 1983-1986 at the study site.

Grass, forb and woody species selected for this study are common to rangelands in the Monte Phytogeographical Province. Dominance of any of these groups in a particular area would be determined at least in part by fire and grazing history, as recently described in a state-and-transition model of vegetation dynamics (21). Under exclosure or light grazing, *Stipa clarazii* Ball.* and *Poa ligularis* Nees ex Steud. are examples of dominant, C3 desirable grasses in the community; both are highly competitive in the absence of grazing and thought to be part of the pristine vegetation (13, 36). However, where moderate grazing has been continuous, these species have been replaced by other C3 desirable perennial grasses, mainly *Stipa tenuis* Phil. and *Piptochaetium napostaense* (Speg.) Hack (21). Other common perennial grasses in the region include desirable C3 *Bromus brevis* Nees, *Stipa neaei* Nees ex Steud., *S. papposa* Nees, C4 *Pappophorum subbulbosum* Arechav. and *Sporobolus cryptandrus* (Torr.) A. Gray. The intermediate C3 *S. speciosa* Trin. & Rupr., *Melica bonariensis* Parodi, C4 *Aristida pallens* Cav., *A. spegazzinii* Arechav. and *A. trachyantha* Henrard are also present. If exposed to heavy, continuous grazing, desirable perennial grasses are replaced by undesirable perennial grasses like C3 *S. trichotoma* Nees

Continuous lack of fire or low fire frequency, heavy grazing, availability of shrub propagules and conditions favouring shrub seedling establishment have determined replacement of desirable perennial grasses by annual grass (*Bromus mollis* L.) or forb species (*Medicago minima* (L.) Grufberg and *Erodium cicutarium* (L.) L'Her. ex Aiton) (24, 21). At this stage of ecosystem degradation, dominant components of the woody layer are deciduous trees [e.g., *Geoffroea decorticans* (Gill. ex Hook. & Arn.) Burkart]; evergreen, perennial shrubs [e.g., *Brachyclados lycioides* Don, *Condalia microphylla* Cav., *Chuquiraga erinacea* D. Don, *Larrea divaricata* Cav. and *Schinus fasciculatus* (Griseb.) Johnston], and deciduous perennial shrubs [e.g., *Lycium chilense* Miers, *Prosopidastrum globosum* (Gill. ex Hook. & Arn.) Burkart and *Prosopis alpataco* Phil.] (21).

The region is a typical plain; soil ranges from loamy and loam-sandy to loam-clay-sandy. Several physical and chemical characteristics at the study site have been reported (28).

Phenological observations were made on the species listed in Figs. 2 to 9, every 7-40 days, from May 1983 to May 1986. They were

---

*Even though *S. clarazii* and *S. longiglumis* Phil. have been cited sometimes as synonyms, Torres (52) has advised use of *S. clarazii* instead of *S. longiglumis* until further studies confirm their status. Therefore, except in original references, only *S. clarazii* will be used throughout this paper.

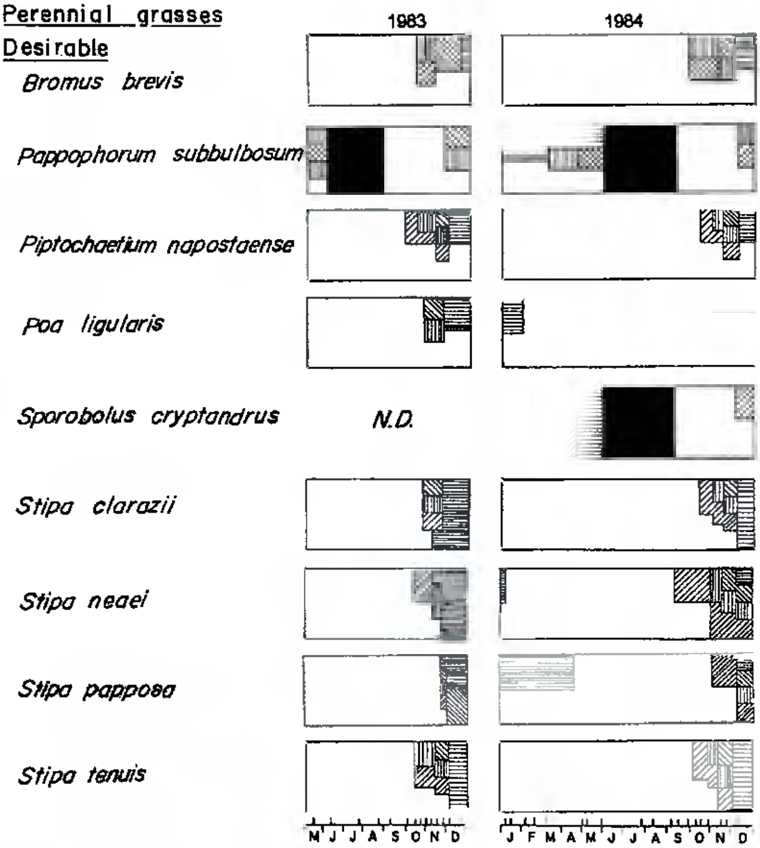

Fig. 2.– Phenological stages of desirable perennial grasses at a site typical of rangelands in the Monte Phytogeographical Province in semiarid Argentina during 1983 and 1984. Phenological stages are: ⠿ seed, ⊠ germination, ☐ sprouting for woody species, vegetative for grasses and forbs, ▨ stem elongation, ☐ boot stage, ▥ flowering, ▧ fructification (incipient, green and/or mature fruits), ▤ seed dispersal/fruit fall, ⠶ leaf fall/senescence, ■ dormancy. Sampling dates within each year are shown as vertical lines right above the month line in the abscissa. The number of phenological stages at any sampling date can be obtained from the Y axis by adding up the number of different shadings on that date. N.D.=Not determined.

taken within more than one-year-old exclosures (15 ha) to domestic herbivory, following the phenological keys of Distel & Peláez (20). At each sampling, all phenological stages of each species were carefully registered by walking through the exclosures. Variability in the occurrence of any given phenological stage among years will only be reported after comparison of similar sampling dates in these years.

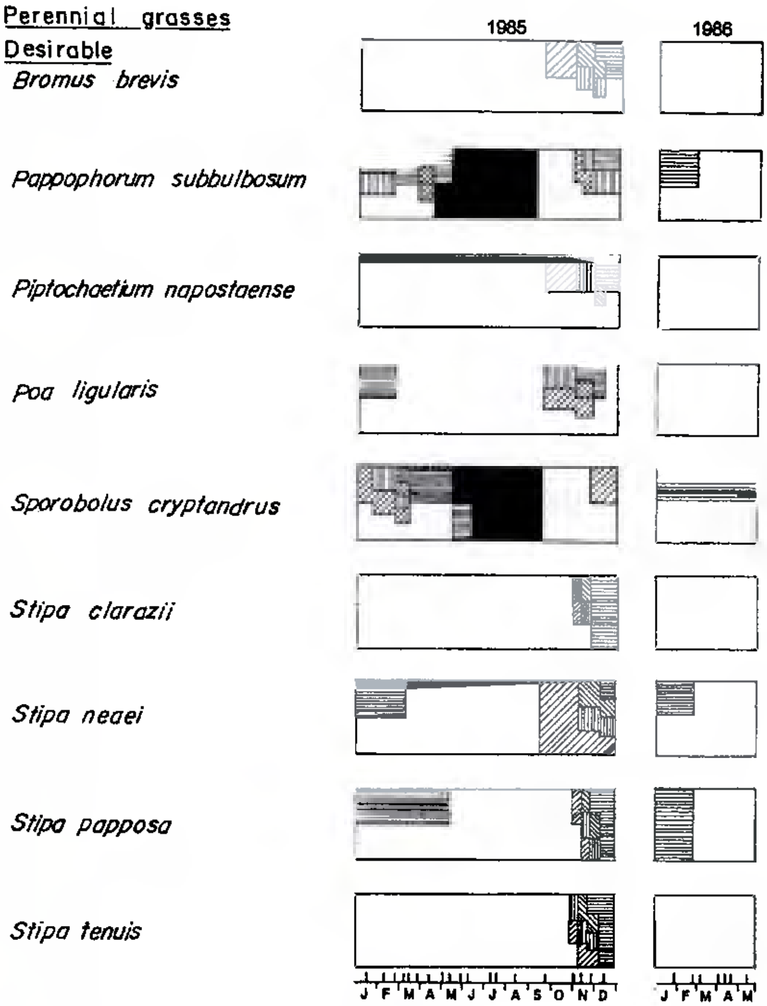

Fig. 3.– Phenological stages in desirable perennial grasses at a site typical of rangelands in the Monte Phytogeographical Province in semiarid Argentina during 1985 and 1986. For information on symbols, samplings, etc., see explanation of Figure 2.

RESULTS & DISCUSSION

Perennial grasses. Except for *Pappophorum subbulbosum*, *Sporobolus cryptandrus* and *Aristida* species, perennial grasses listed in Figs. 2 to 5 have usually been classified as autumn-winter-spring species because they vegetate during these seasons (13). *Pappophorum subbulbosum, S. cryptandrus* and the *Aristida* species have often

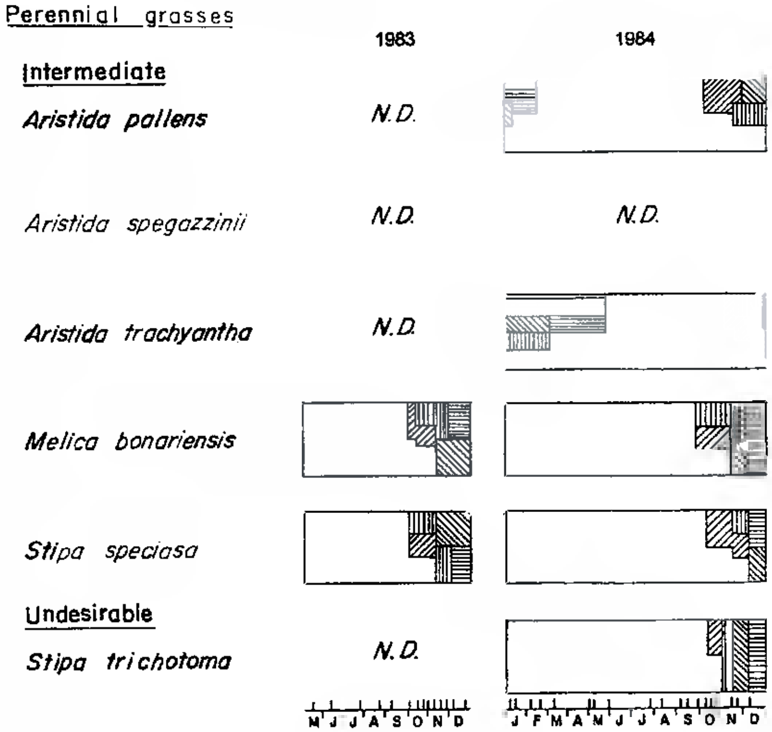

Fig. 4.– Phenological stages of intermediate and undesirable perennial grasses at a site typical of rangelands in the Monte Phytogeographical Province in semiarid Argentina during 1983 and 1984. For information on symbols, samplings, etc., see explanation of Figure 2.

been categorized as spring-summer species because they remain vegetative during these periods (13). However, high rainfall values during December 1984-January 1985 (354 mm, Fig. 1) or February and March 1984 (280 mm, Fig. 1) may have contributed to the extension of tillering during summer in the autumn-winter-spring species or towards the end of spring, summer and even autumn in the spring-summer perennial grasses, respectively (Figs. 2-5). A similar extension of tillering during summer is reported in *P. napostaense*, *S. tenuis* and *P. subbulbosum* (20), and in *Pappophorum caespitosum* (17). No tillering occurred during January and the first half of February in *S. papposa* in 1986; rainfall during this period was < 15% of that during the same period in 1984 and 1985 (Fig. 1). In agreement with this observation, it is reported (7) that phenological development was interrupted and the reproductive period did not start

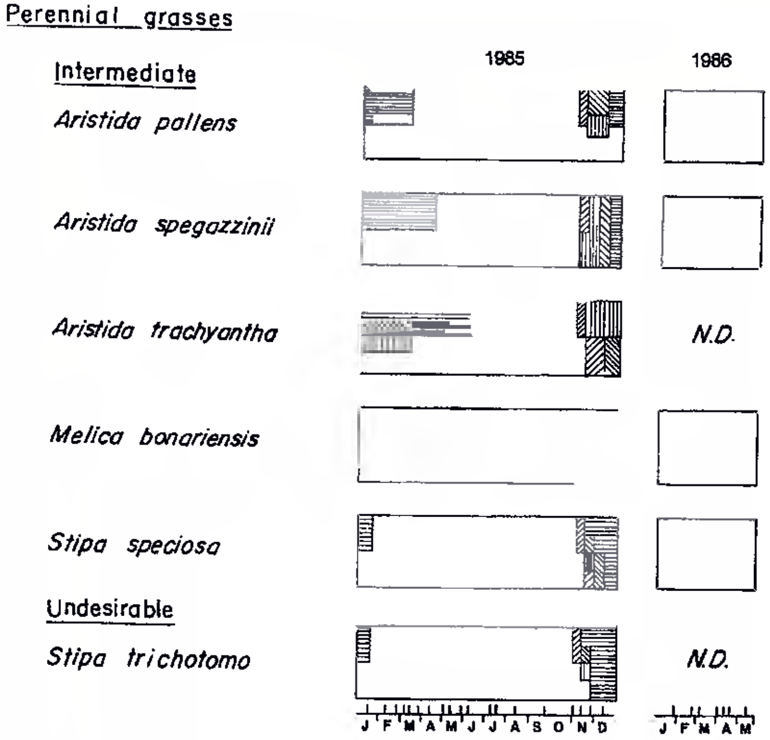

Fig. 5.– Phenological stages of intermediate and undesirable perennial grasses at a site typical of rangelands in the Monte Phytogeographical Province in semiarid Argentina during 1985 and 1986. For information on symbols, samplings, etc., see explanation of Figure 2.

or failed shortly after initiation in *P. ligularis*, *S. speciosa* and *S. tenuis* when water in the upper soil was depleted in late spring and summer in an arid ecosystem of the southern portion of the Monte Phytogeographical Province. The extent of tillering on an annual basis in these grasses may thus be closely tied up to rainfall. Dickinson & Dood (19) cautioned about classifying species as strictly cool- or warm-season since some exhibit characteristics of both groups. Pulses of activity synchronic with water inputs have also been reported for several grasses in communities of northern Patagonia (48, 6). Additional tillering during wet years could add to the available forage. Olson & Richards (38) reported that in wet years or at sites with higher soil moisture availability into summer, contribution of axillary tillers to late spring and summer production would have been considerably greater than what they observed in *Agropyron desertorum* (Fisch. ex Link) Schult.

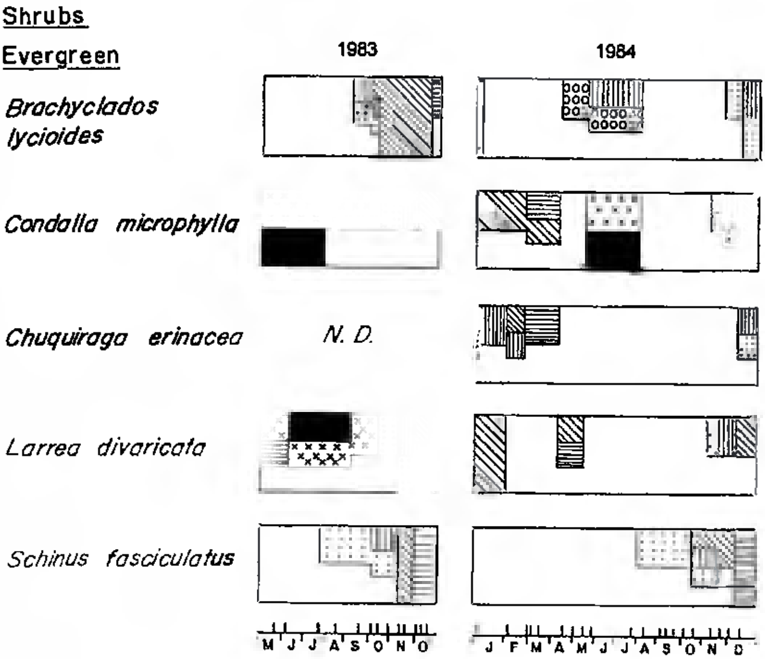

Fig. 6.– Phenological stages of evergreen shrubs at a site typical of rangelands in the Monte Phytogeographical Province in semiarid Argentina during 1983 and 1984. For information on symbols, samplings, etc., see explanation of Figure 2.

Periods of flowering, fruit production, seed dispersal or dormancy in the perennial grasses are similar to the general patterns given for these species (3, 13, 20). However, a drier period during April-June in 1985 (41.3 mm) than in 1984 (160.5 mm) and 1983 (127.7 mm) may have contributed to an advancement of the plant dormancy stage in *P. subbulbosum* in 1985 (Figs. 1-3). Dormancy appears to be a major mechanism for coping with seasonal drought and extended water deficits in mid-continental regions such as the North American Great Basin (30, 46). As such, it reduces exposed leaf surfaces to water loss and heat gain during periods of water deficits (10). Also, stem elongation in *P. napostaense* and *P. subbulbosum*; flowering in *S. papposa, S. speciosa* and *S. tenuis*; fructification in *P. subbulbosum, P. ligularis, S. clarazii, S. papposa* and *S. speciosa*, and seed dispersal in *A. pallens, M. bonariensis, P. subbulbosum, S. cryptandrus, S. clarazii, S. neaei, S. papposa, S. speciosa* and *S. trichotoma* occurred earlier in the drier springs of 1983 and/or 1985 compared to that in 1984 (Figs. 2-5). Rainfall between September and December (Fig. 1)

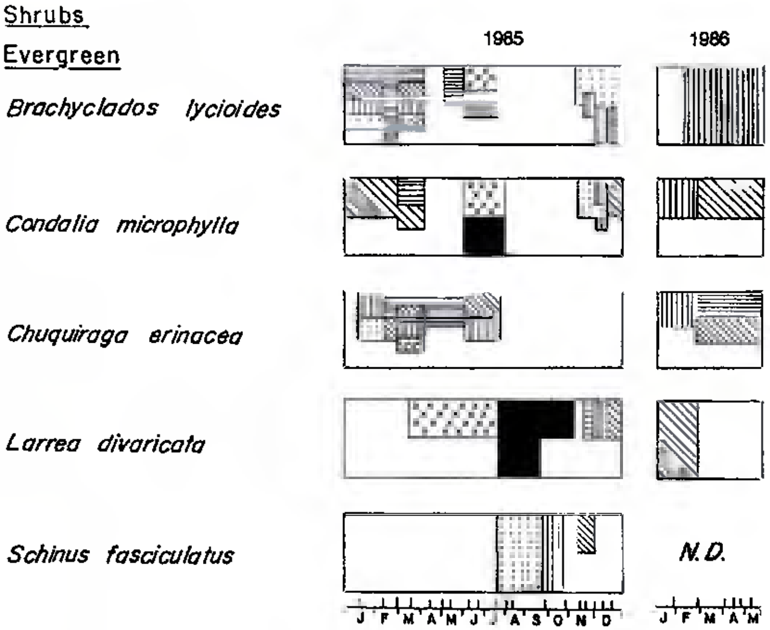

Fig. 7.– Phenological stages of evergreen shrubs at a site typical of rangelands in the Monte Phytogeographical Province in semiarid Argentina during 1985 and 1986. For information on symbols, samplings, etc., see explanation of Figure 2.

was 104 mm in 1983, 160 mm in 1985 and 300 mm in 1984. Maintenance of high soil water potentials by irrigating throughout the growing season has also retarded phenological development by about 10 days in *Bromus tectorum* L. and *Poa sandbergii* Vasey (32). Knowledge of the advancement of these phenological stages during dry periods in these species is important in adjusting grazing management accordingly if natural reseeding is to be favored.

Our results, disagree with those of Jones (31), who reported that water deficits delay flowering in perennials. Adaptive shifts in the timing of flowering are well known to occur in annuals as a result of water stress (47, 43, 4, 31, 49). For example, water stress accelerated the transition to flowering in *Bromus fasciculatus* C. Presl. (by 1-2 days) and in *Brachypodium distachyon* (L.) Beauv. (by 4-6 days); and diaspore maturation in these species (4); it advanced flowering by up to a week in *Triticum aestivum* cv. Gabo (2). Time to heading was also 3.5 days shorter under rainfed than under irrigated conditions in *Triticum aestivum* L. in a Mediterranean environment (53). Under terminal drought, other studies show a positive correlation between early heading and grain yield in *Pennisetum americanum* (L.) Leeke

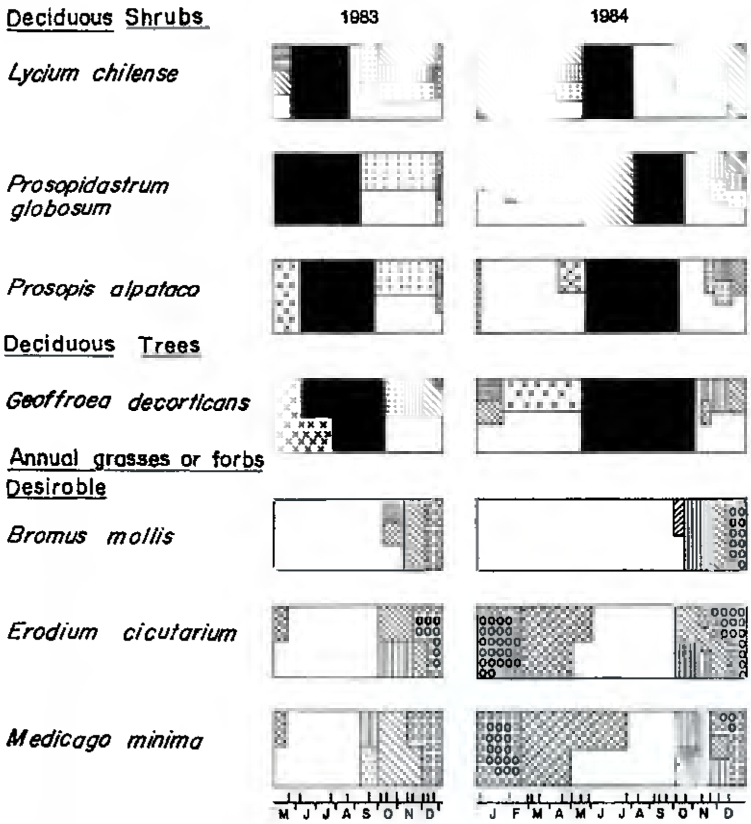

Fig. 8.– Phenological stages of deciduous shrubs or trees and desirable annual grasses or forbs at a site typical of rangelands in the Monte Phytogeographical Province in semiarid Argentina during 1983 and 1984. For information on symbols, samplings, etc., see explanation of Figure 2.

and *Hordeum vulgare* L. (8, 54). The ability of plants to alter the phenotypic expression of their genotype in response to the environment may enhance individual plant capacity to survive and reproduce (50).

Flowering in *M. bonariensis* and *S. trichotoma*, on the other hand, was advanced in the wet spring of 1984 in comparison to the drier ones of 1983 or 1985 (Figs. 4 & 5). Inflorescence exsertion in *Sporobolus flexuosus* (Thurb.) Rydb. was delayed by about 2 months partially as a result of 38 mm less rainfall (27). A wet spring in 1984 extended the periods for stem elongation in *P. subbulbosum*, *S. papposa* and *S. speciosa*, flowering in *A. pallens* and *S. papposa*, and fructification in *A. pallens* in comparison to the drier 1983 and/or 1985 (Figs. 2-5). On the other hand, low rainfall between November and February in

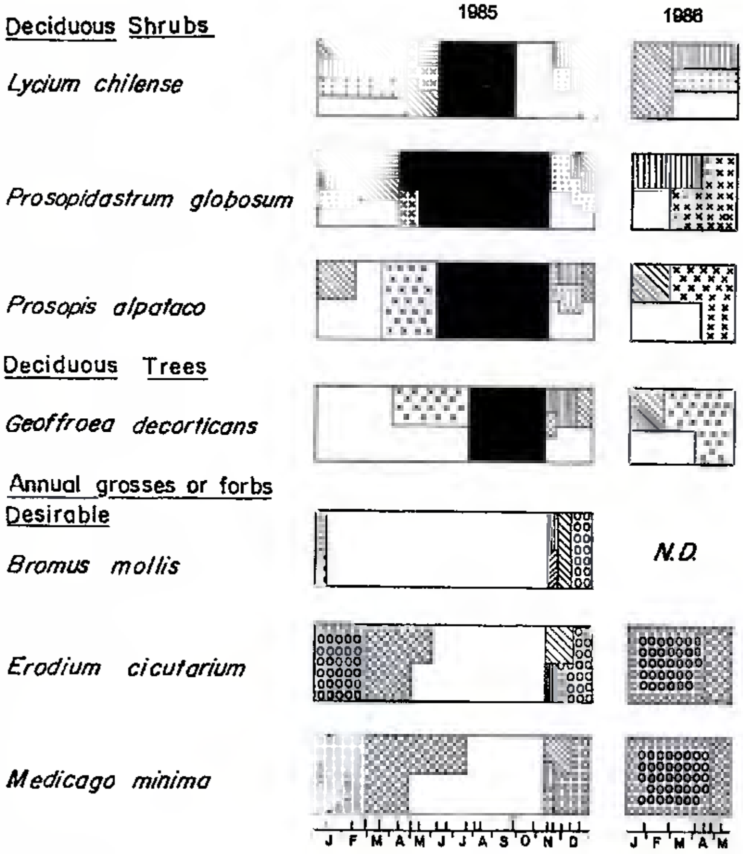

Fig. 9.– Phenological stages of deciduous shrubs or trees and desirable annual grasses or forbs at a site typical of rangelands in the Monte Phytogeographical Province in semiarid Argentina during 1985 and 1986. For information on symbols, samplings, etc., see explanation of Figure 2.

1985/6 (76.3 mm) when compared to rainfall in the same period in 1984/5 (419.4 mm) and 1983/4 (259.9 mm) may have contributed to shorten the extent of seed dispersal in the drier period in *A. pallens*, *P. subbulbosum* and *P. ligularis* (Figs. 1-5).

Woody species. Similar to previous reports (13, 20), sprouting started by early to mid spring in the woody species (Figs. 6 to 9). Activity of deep-rooted woody species was triggered when temperature began to increase in early spring by using the water stored deep in the soil during the rainy period (48, 6). During wet summers (December 1984-January 1985 and February-March 1984: Fig. 1), however, sprouting extended until the end of this season or even early autumn in the deciduous *(Geoffroea decorticans, Lycium chilense, Prosopidastrum globosum, Prosopis alpataco)* or evergreen *(Brachyclados lycioides, Condalia microphylla, Chuquiraga erinacea, Larrea divaricata, Schinus fasciculatus)* species (Figs. 6-9). Timing for the vegetative stage may thus go well beyond limits given for these species (13, 20). Our results agree with those reported in *Artemisia tridentata* (23) and in shrubs of the Great Basin where a longer leaf development period was obtained with increased soil moisture levels (12). Scant rain suppressed vegetative activity in *Larrea tridentata* (Sesse & Moc. ex Dc.) Cov. (45), although temperature appears to be a major environmental variable controlling activity in this species when water is not limiting (15, 16). Summer rains can trigger summer growth in this species in the Mojave Desert if precipitation is > 25 mm (5). This can be attributed to its lateral shallow roots in addition to its deep main root (33).

The sensitive response of lateral roots to small amounts of rain allows the plant to take advantage of increased moisture supply at the soil surface following rain. An additional active growth period in *L. tridentata* was observed in late fall (November and December) associated with an unusually warm and moist December (45). It appears that *Larrea* may have the genetic potential for multiple growth patterns, depending on climatic conditions; shifts of growth towards early spring or late summer may depend on favourable temperature and rain (16). A strong relationship between soil moisture and phenological events is also reported for *Lycium andersonii* (1). Production of vegetative structures has been fostered by higher levels of water availability in the desert shrubs *Jatropha cinerea* (Ortega) Muell. Arg. and *J. cuneata* Wiggins & Rollins (35). Leaf flushing of 49 woody species (either evergreen, semideciduous or fully deciduous) also started following the attainment of seasonal minima in pre-dawn leaf water potential (55).

The reproductive stage has been reported to occur during spring and/or summer in these species (20, 13, 3, 34). Cano (13) and Distel & Peláez (20), for example, confined flowering to December in other *Prosopis* species. In our study, the boot and flowering stages occurred during the previous 2 months in *P. alpataco* (Figs. 8 and 9). The reproductive stage for the species shown in Figs. 8 and 9 occurred thus at later times than those reported (3, 13, 20). Drier conditions during early spring (September and October) in 1983 (58.5 mm) than in 1984 (137 mm) and/or 1985 (115.6 mm) may have contributed to advance the boot stage in *P. globosum;* the boot, flowering and reproductive phases in *L. chilense*, and the reproductive stage in *B. lycioides* (Figs. 1 and 6-9). These results are similar to those (14) obtained in *Prosopis chilensis* (Mol.) Stuntz which advanced the boot developmental stage as the growing season became drier in semiarid Argentina. Production of flowers in the spiny desert shrub *Fouquieria diguetti* (Tiegh.) I.M. Johnstone was greater during the dry season (35). These authors suggested that this species can optimize use of resources through differentially translocating water for vegetative and sexual structures when it is available, and for sexual structures when it is not, thereby assigning energy to reproduction mechanisms. *Jatropha cinerea* and *J. cuneata* interrupt flowering and fructification due to soil moisture reduction in the desert scrub community in Mexico (35). This response also occurs in trees and tall shrubs of the tropical semi-arid vegetation of Venezuela where the short rainy season seems to be responsible for the initiation and synchrony of flowering (29). Tropical trees of Costa Rica and *Tabebuia neochrysantha* A. Gentry, a deciduous forest species, show the same pattern (39, 44).

On the other hand, fructification in spring was advanced in the wet 1984 when compared to the dry 1983 in *S. fasciculatus* (Figs. 6 and 7). The desert tree *Bursera microphylla* A. Gray needs a soil moisture threshold to bloom, but it showed abundant flowering when high soil moisture was available (35). Aramayo et al. (3) reported the period for the earliest and latest flowering dates during a 3-year-period in *G. decorticans*, *L. chilense* and *P. globosum* in semiarid Argentina. Although they recognized variability in the flowering date of these species from year to year, they did not relate this variability to climatic parameters.

The beginning of autumn (March and April) was wetter in 1984 (155.5 mm) than in 1985 (93.3 mm) (Fig. 1). This may have contributed to extend the reproductive phase during this period in 1984 in *P. globosum* (Figs. 8 and 9).

Drier conditions during August and September in 1983 (22.5 mm) than in 1984 (75.8 mm) and 1985 (44.3 mm) may have contributed to extend the period of leaf fall in *C. microphylla* (Figs. 1, 6 & 7). Leaf fall occurred in *L. divaricata* during at least May and June in 1983 and 1985 but it was not observed in these months in 1984 (Figs. 6 & 7); less rainfall during this period in 1983 (59.2 mm) and 1985 (28.0 mm) than in 1984 (118.5 mm) may help explain this observation (Fig. 1). Leaf shedding occurred as soon as soil moisture decreased in *Fouquieria diguetti*, a desert scrub community perennial (35). In 49 evergreen, semideciduous or fully deciduous woody species leaf fall coincided with the attainment of seasonal minima in leaf water potential (55).

Overall, phenological development in *Geoffroea decorticans* conforms to that reported by Mújica et al. (37) in an area with a long-term mean rainfall (583 mm) higher than that at our study site (455 mm); sprouting started by the end of October in 1984 and 1985 (Figs. 8 & 9), a month when rainfall was similar in both years (Fig. 1). However, in *G. decorticans* (37), *Prosopis flexuosa* and *P. caldenia* (20), and *P. chilensis* (14) the beginning of sprouting does not appear to be influenced by rainfall; this could be partially due to their deep and extensive root system (51, 22, 42, 14). However, *Condalia microphylla*, a shrub with relatively shallow root system (42), initiated sprouting by early August during 1983-1985 (Figs. 6 & 7). Rainfall during the previous month (July), had been null in 1983, 67.0 mm in 1984 and 112.5 mm in 1985 (Fig. 1).

Annual grasses or dicots. High rainfall during early 1984 and 1985 (> 210 mm in January and February: Fig. 1) contributed to the germination of *Medicago minima* and *Erodium cicutarium* at the beginning of March in both years (Figs. 8 & 9). Germination of these species occurred later in 1986 than in the two previous years, very likely because of less rainfall during January-March of that year (Fig. 1). Germination was delayed until early May in both species (26) when rainfall during January-April was less than 30 mm in central, semiarid Argentina. Regulation mechanisms thus restrict germination of seeds of winter annuals to periods of comparatively abundant moisture, coinciding with favourable temperatures (5). Prior to germination, seeds of these species are scarified by wide daily temperature oscillations at the soil surface during summer, and freezing and thawing cycles during autumn at the study site (25).

Mid-spring (October-November) was wetter in 1984 (106.5 mm) and 1985 (90.6 mm) than in 1983 (61 mm) (Fig. 1); this may have contributed to the extension of the boot and flowering stages later into the season in the wetter years in *M. minima* (Figs. 8 & 9). Flowering was also observed during mid-spring in *M. minima* in an area with rainfall concentrated during autumn and spring during a yearly cycle, and an annual average rainfall of 574,9 mm (3).

Plant death in *M. minima* and *E. cicutarium* had not occurred by the end of November in 1984 and 1985. The earlier plant death reported for these species (26) may be partially attributed to the drier mid-spring in their study (30 mm rainfall in both October and November) than in ours (>90 mm rainfall in the same period). In annuals, the onset of senescence can be induced and accelerated by water stress resulting in a shorter growth cycle (4). Other than germination time and timing of plant death, the phenological development shown in Figs. 8 & 9 for *M. minima* and *E. cicutarium* is similar to that reported for these species in the Southern Caldenal (13,20,26). Germination and seedling establishment in *Bromus mollis* starts by early or mid-summer if this season is wet, as was observed during the wet summers of 1984 and 1985 (Figs. 1, 8 & 9).

Species-specific responses of phenology to soil moisture, scant rain, air temperature, and soil nutrient availability, was shown for main plant components of an arid ecosystem in north-eastern Patagonia (16). In our study, air temperatures were very similar among years during the period of study (Fig. 1) and rainfall appeared to be a major environmental factor affecting phenology. However, the interaction among several abiotic factors which can potentially exert some control on phenology (i.e., 7) may distinctly affect phenological development among years within each species. This could help explain the interannual variation of phenological events in each of the species studied.

A species must be able to cope with extended periods of intra-seasonal drought (i.e., 28) to be successful in the Monte Phytogeographical Province. The temporal plasticity in the phenology of the perennial or annual grasses, herbaceous dicots or woody species suggests that they are well adapted to their environment. This plasticity has been maintained when the phenology of some of these species has been reported for much drier regions of Argentina [(mean annual precipitation: 175 mm: (7)]. Although the phenology of the species was compared for years with total annual rainfall similar to or above the long-term mean, it must be emphasized that both wet and dry years are normal in the long-term weather pattern in the Monte Phytogeographical Province (28).

LITERATURE CITED

1. Ackerman TL, EM Romney, A Wallace, J Kinnear, *Great Basin Naturalist Memoirs. Brigham Young University* 4 (1980) 4
2. Angus JF, MW Moncur, *Aust J Agric Res* 28 (1977) 177
3. Aramayo E, A Valle, A Andrada, S Lamberto, *Parodiana* 8 (1993) 265
4. Aronson J, J Kigel, A Shmida, J Klein, *Oecologia* 89 (1992) 17
5. Beatley JC, *Ecology* 55 (1974) 856
6. Bertiller MB, *Acta Oecologica, Oecologia Generalis* 5 (1984) 365
7. Bertiller MB, AM Beeskow, F Coronato, *J Arid Environ* 21 (1991) 1
8. Bidinger FR, V Mahalakshmi, GDP Rao, *Aust J Agr Res* 38 (1987) 37
9. Briske DD, JH Richards, *In* DJ Bedunah, RE Sosebee, eds, *Wildland plants: Physiological ecology and developmental morphology.* Soc Range Manage, Denver, Colo (1995) p 635
10. Brown RW, *In* DJ Bedunah, RE Sosebee, eds, *Wildland plants: Physiological ecology and developmental morphology.* Soc Range Manage Denver, Colo (1995) p 291
11. Cabrera AL, *In* EF Ferreira Sobral, ed, *Enciclopedia Argentina de Agricultura y Jardineria.* ACME, Buenos Aires (1976) p 1
12. Caldwell MM, *In*: BF Chabot, HA Mooney, eds, *Physiological Ecology of North American Plant Communities.* Chapman and Hall, New York (1985) p 198
13. Cano E, *Pastizales naturales de La Pampa. Descripción de las especies más importantes*(1988). Convenio AACREA, Provincia de La Pampa, Buenos Aires.

14. Caro LA, LF Hernández, V Lauric, *Yvyrareta* 8 (1997) 3
15. Chew R, A Chew, *Ecol Monogr* 35 (1965) 355
16. Cunningham GL, JP Syversten, JF Reynolds, JM Willson, *Oecologia* 40 (1979) 113
17. Dalmasso AD, *Multequina* 3 (1994) 9
18. De Fina AL, *In* LR Parodi, ed, *Enciclopedia Argentina de Agricultura y Jardinería. El cultivo de las plantas útiles*. ACME, Buenos Aires (1964) p 15
19. Dickinson CE, JL Dodd, *Amer Midland Naturalist* 96 (1976) 367
20. Distel RA, DV Peláez, *IDIA* 441-444 (1985) 35
21. Distel RA, RM Bóo, *In* NE West, ed, *Proc. of the Fifth International Rangeland Congress Rangelands in a sustainable biosphere*, Society for Range Management, Denver, Colo (1996) p 117
22. Fernández OA, T Montani, RA Distel, *Interciencia* 13 (1988) 2 5
23. Fisser HG, Phenology. *In* B Mc Arthur, BL Welch, eds, *General Technical Report Intermountain Research Station*, Int-200 (1986) p 314
24. Fresnillo Fedorenko DE, OA Fernández, CA Busso, *In* A Gaston, M. Kernik, H. Lehoveron, eds, *Proc. Symp. Grazing, a challenge for development and environment*, International Rangeland Congress, Montpellier, France(1991) p 372
25. Fresnillo Fedorenko DE, OA Fernández, CA Busso, *Turrialba* 44 (1994) 95
26. Fresnillo Fedorenko DE, OA Fernández, CA Busso, OR Elía, *J Arid Environ* 33 (1996) 409
27. Gibbens RP, *J Range Manage* 44 (1991) 86
28. Giorgetti HD, OA Montenegro, GD Rodríguez, CA Busso,T Montani, MA Burgos, AC Flemmer, MB Toribio,SS Horvitz, *J Arid Environ* 36 (1997) 623
29. Guevara De Lampe M, Y Bergeron, R Mcneil, A.Leduc, *Biotropica* 24 (1992) 64
30. Harris GA, GS Campbell, 1981. *In* DD Evans, JL Thames, eds, *Water in desert ecosystems*, USIBP Synthesis Series 11. Dowden, Hutchinson and Ross, Inc. Stroudsburg (1981) p 59
31. Jones HG, *Plants and microclimate. A quantitative approach to environmental plant physiology*. Cambridge University Press, Cambridge (1992)
32. Link SO, GW Gee, JL Downs, J *Range Manage* 43 (1990) 506
33. Ludwig JA, *In* JK Marshall, ed, *The below-ground ecosystem: a synthesis of plant-associated processes*, Colorado State University, Ft. Collins, Colo (1977) p 85
34. Marco DE, AA Calviño, SA Páez, *J. Arid Environ* 44 (2000) 327
35. Maya Y, L Arriaga, *J Arid Environ* 34 (1996) 23
36. Moretto AS, RA Distel, *Plant Ecology* 130(1997) 155
37. Mujica MB, LM Malla, MC Mocchi, ME García, *RIA* 23 (1992) 53
38. Olson BE, JH Richards, *Oikos* 51 (1988) 374
39. Opler PA, GW Frankie, HG Baker, *J Biogeogr* 3 (1976) 231
40. Papadakis J, *El Clima*. Editorial Albatros, Buenos Aires, Argentina (1980), p. 377
41. Parodi LR, *In* LR Parodi, ed, *Enciclopedia Argentina de Agricultura y Jardinería, El cultivo de las plantas útiles*. Vol.2 (Primera parte), Editorial Acme, Buenos Aires (1964) p. 1
42. Peláez DV, RA Distel, RM Bóo, OR Elía, MD Mayor, *J Arid Environ* 27 (1994) 71
43. Rathcke B, EP Lacey, *Annu Rev Ecol Syst* 16 (1985) 179
44. Reich PB, R Borchert, *Ecology* 63 (1982) 294
45. Sharifi MR, FC Meinzer, ET Nilsen, PW Rundel, RA Virginia, WM Jarrell, DJ Herman, PC Clark, *Amer J Bot* 75 (1988) 1163
46. Smith SD, RS Nowak, *In* CB Osmond, LF Pitelka, GM Hidy, eds, *Plant Biology of the Basin and Range*, Springer-Verlag. Berlin (1990) p. 179
47. Solbrig OT, MA Barbour, J Cross, G Goldstein, CH Lowe, J Morello, TW Yang, *In* GH Orians, OT Solbrig, eds, *Convergent Evolution in warm deserts*, Hutchinson and Ross, Stroudsburg (1997) p. 67
48. Soriano A, *Producción Animal* 8 (1981) 38
49. Steyn HM, N Van Rooyen, MW Van Rooyen, GK Theron, *J Arid Environ* 33 (1996) 49

50. Sultan SE, *Evol Biol* 21 (1987) 127
51. Talmon LG, MB Mújica, *Resúmenes XX Jornadas Argentinas de Botánica. Sociedad Argentina de Botánica,* Salta (1985)
52. Torres MA, Revisión del género *Stipa* (Poaceae) en la Provincia de Buenos Aires. Monografia 12. Ministerio de la Producción. Comisión de Investigaciones Cientificas (CIC), Buenos Aires (1993)
53. Van Den Boogaard R, EJ Veneklaas, JM Peacock, H Lambers, *Plant Soil* 181 (1996) 251
54. Van Oosterom EJ, E Acevedo, *Euphytica* 2 (1992) 15
55. Williams RJ, BA Myers, WJ Muller, GA Duff, D Eamus, *Ecology* 78 (1997) 2542