

Abstract

Phenological stages of several desirable, intermediate or undesirable perennial grasses, evergreen or deciduous shrubs, deciduous trees or desirable annual grasses or forbs are described and related to rainfall at a site typical of rangelands in the Monte Phytogeographical Province in temperate, semiarid Argentina. Studies were concentrated during 1984 and 1985 although observations were also taken during part of 1983 and 1986. Greater levels of soil water availability 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. Plants of these species maintained green leaves during the whole year during 1984 which was wetter than 1983 and 1985. This cautions about strictly classifying these perennial grasses as either cool- or warm-season species because they can exhibit characteristics of both groups. Stem elongation, flowering, fructification and/or seed dispersal in several autumn-winter-spring and spring-summer perennial grasses, and the boot stage, flowering and/or the reproductive stage of development in some woody species occurred earlier in the drier springs of 1983 and/or 1985 in comparison to that in 1984. However, flowering in *Melica bonariensis* Parodi and *Stipa trichotoma* Nees and the reproductive stage in *Schinus fasciculatus* (Griseb.) Johnston were advanced, and stem elongation, flowering and/or fructification in *S. papposa* Nees, *S. speciosa* Trin. & Rupr., *Pappophorum subbulbosum* Arechav. and *Aristida pallens* Cav. were extended later into the season during the

wetter 1984 when compared with the drier 1983. During wet summers, like those in 1984 and 1985, sprouting (which usually starts by early to mid-spring) can extend towards the end of summer-early autumn in the evergreen or deciduous woody species.

Key words: Phenology, Semiarid Argentina, Annual and perennial grasses, Annual forbs, Shrubs and trees.

INTRODUCTION

Knowledge of when a certain plant species will reach a specific developmental stage can assist range managers in timing their management practices and vegetation scientists in choosing the optimal time for sampling in different regions. Comparative phenological development has received some attention in herbaceous and woody species in the Southern Caldenal, a Phytogeographic Region of about 40000 km² in central, semiarid Argentina (CANO, 1988; CARO *et al.*, 1997; DISTEL & PELAEZ, 1985; MUJICA *et al.*, 1992). However, these studies have only provided some general information on the phenology of these species or been limited to a few species.

Rangelands in the Monte Phytogeographical Province, south of the Southern Caldenal, cover about 528000 km² in central Argentina and experience low and highly variable rainfall (long term range 100-400 mm per annum) (PARODI, 1964). Since precipitation can be a critical factor in plant phenology in arid and semiarid areas (BEATLEY, 1974), species commonly found in these rangelands will have reproductive strategies that enable

them to survive these conditions. This paper therefore focuses on providing a more detailed description or additional information of phenological events in several herbaceous and woody species of the "Monte" and their relationship to rainfall.

MATERIALS AND METHODS

Area description

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

The general climate, vegetation and soil characteristics of the region have been reported by CABRERA (1976), DE FINA (1964) and PARODI (1964). The climate is temperate semiarid, mean annual temperature is 14.6 °C, and mean monthly temperatures of the coldest (July) and warmest (January) months varie between 3-12 °C and 19-27 °C, respectively. Absolute minimum and maximum temperatures have varied between -5 to -17 °C and 35 to 46 °C. The mean relative humidity is 60%. Winds have an annual mean of 13 km h⁻¹. Rainfall is concentrated during spring and fall, and during 1983-1986 (fig. 1) was provided by a meteorological station located at the study site. Mean annual water deficit varies between 400 to 800 mm.

The community is characterized by an open shrubby layer which includes herbaceous species of different desirability for cattle production. Cattle raising on natural vegetation is the most important economic activity in the study region (CABRERA, 1976). In

this study, annual or perennial grass and forbs species of the herbaceous layer were categorized into desirable (highly preferred), intermediate (grazed when desirable species are not available) or undesirable (only cut off when a better forage is not available) on the basis of their acceptability by cattle. Woody species were classified as either evergreen or deciduous.

Grass, forb and woody species selected for the study are common to rangelands in the Monte Phytogeographical Province. Dominance of a particular species group in any given area, however, would be determined at least in part by fire and grazing history as has been recently described by Distel & Bóo (1996) in their state-and-transition model of vegetation dynamics. Under exclosure or light grazing conditions, *Stipa clarazii* Ball.* and *Poa ligularis* Nees ex Steud. are an example of dominant, C3 desirable perennial grass

*Even though *S. clarazii* and *S. longiglumis* Phil. have been cited sometimes as synonymous, Torres (1993) has advised use of *S. clarazii* instead of *S. longiglumis* until further studies confirm if these are either different or the same species. Except in original references, only *S. clarazii* will thus be used throughout this manuscript.

species in the community; both species are highly competitive in the absence of grazing and thought to be part of the pristine vegetation (CANO, 1988; MORETTO & DISTEL, 1997). At sites where moderate grazing has been continuous, however, these species have been replaced by other C3 desirable perennial grasses, mainly *Stipa tenuis* Phil. and *Piptochaetium napostaense* (Speg.) Hack. Other common perennial grasses in the region include the desirable C3 *Bromus brevis* Nees, *Stipa neaei* Nees ex Steud. and *S. papposa* Nees, and C4 *Pappophorum subbulbosum* Arechav. and *Sporobolus cryptandrus* (Torr.) A. Gray, and the intermediate C3 *S. speciosa* Trin. & Rupr. and *Melica bonariensis* Parodi and C4 *Aristida pallens* Cav., *A. spegazzinii* Arechav. and *A. trachyantha* Henrard. If exposed to heavy, continuous grazing, desirable perennial grasses have been replaced by undesirable perennial grasses like the C3 *S. trychotoma* Nees. Under continuous lack of fire or low fire frequency, heavy grazing, availability of shrub propagules and conditions favouring shrub seedling establishment, sites dominated by desirable perennial grasses have been converted to a shrubland and these grasses have been replaced by undesirable ones or annual grass (*Bromus mollis* L.) or forbs (*Medicago minima* (L.) Grufberg and *Erodium cicutarium* (L.) L'Her. ex Aiton) (FRESNILLO FEDORENKO et al., 1991). At this stage of ecosystem degradation, dominant components of the woody layer are deciduous tree species like *Geoffroea decorticans* (Gill. ex Hook. & Arn.) Burkart; evergreen, perennial shrubs like *Brachyclados lycioides* Don,

Condalia microphylla Cav., *Chuquiraga erinacea* D. Don, *Larrea divaricata* Cav. and *Schinus fasciculatus* (Griseb.) Johnston, and deciduous, perennial shrubs such as *Lycium chilense* Miers, *Prosopidastrum globosum* (Gill. ex Hook. & Arn.) Burkart and *Prosopis alata* Phil.

Regional topography is typically a plain. Soil texture varies from loamy and loam-sandy to loam-clay-sandy. Average soil pH is 7.6, organic carbon is 0.6%, organic matter is 1% and total nitrogen is 0.006% (GIORGETTI et al., 1997).

Phenological observations

Phenological observations were effected every 15-30 days during 1984 and 1985 although they were also conducted during part of 1983 and 1986. Observations were taken within exclosures to domestic herbivory of more than one-year-old at both sites following the phenological keys reported by DISTEL & PELAEZ (1985). At each sampling time, the most conspicuous phenological stages were taken for each species by walking through the exclosures. Variability in the date of occurrence of any given phenological stage among years will be only reported after comparison of similar sampling dates in these years.

RESULTS AND DISCUSSION

Perennial grasses

With the exception of *Pappophorum subbulbosum*, *Sporobolus cryptandrus* and the *Aristida* species, perennial grasses listed in Fig. 2 have usually been classified as autumn-winter-spring species because of vegetating during these seasons (CANO, 1988). *Pappophorum subbulbosum*, *S. cryptandrus* and the *Aristida* species have often been categorized as spring-summer species because they remain vegetative during these periods (CANO, 1988). 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 (fig. 2). A similar extension of tillering during summer was observed by DISTEL & PELAEZ (1985) in *P. napostaense*, *S. tenuis* and *P. subbulbosum*, and DALMASSO (1994) in *Pappophorum caespitosum*. Tillering was not observed 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). DICKINSON & DOOD (1975) cautioned about classifying species as strictly cool- or warm-season since some species exhibit characteristics of both groups.

Periods of flowering, fruit production, seed dispersal or dormancy in the perennial grasses are coincident with the general

patterns given by ARAMAYO et al. (1993), CANO (1988) and DISTEL & PELAEZ (1985) in these species, and DALMASSO (1994) in *P. caespitosum*. 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 and 2). 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 more than 10 days earlier in the drier springs of 1983 and/or 1985 in comparison to that in 1984; rainfall was 104 mm in 1983, 160 mm in 1985 and 300 mm in 1984 between September and December (fig. 1). Maintenance of high soil water potentials by irrigating throughout the growing season has also retarded phenological development by about 10 days in *Bromus tectorum* and *Poa sandbergii* (LINK et al., 1990). Adaptive shifts in the timing of flowering are well known to occur in annuals as a result of water stress conditions (ARONSON et al., 1992; RATHCKE & LACEY, 1985; SOLBRIG et al., 1977; STEYN et al., 1996). For example, water stress accelerated the transition to flowering in *Bromus fasciculatus* (by 1-2 days) and in *Brachypodium distachyon* (by 4-6 days), and diaspore maturation in these species (ARONSON et al., 1992). Time to heading was also 3.5 days shorter on

average under rainfed than under irrigated conditions in *Triticum aestivum* L. in a Mediterranean environment (VAN DEN BOOGAARD et al., 1996); under terminal drought, other studies have shown a positive correlation between early heading and grain yield in *Pennisetum americanum* (L.) Leeke and *Hordeum vulgare* L. (BIDINGER et al., 1987; VAN OOSTEROM & ACEVEDO, 1992). The ability of plants to alter the phenotypic expression of their genotype in response to the environment may enhance the individual plant's capacity to survive and reproduce (SULTAN, 1987). The phenotypic plasticity to reproductive development and diaspore maturation and subsequent seed dispersal observed in the perennial grasses may be contributing to their adaptation to rainfall unpredictability in the Monte Phytogeographical Province.

Flowering in *M. bonariensis* and *S. trychotoma*, on the other hand, was advanced by several days as the spring became wetter in 1984 in comparison to that drier in 1983 or 1985 (fig. 2). Similarly, inflorescence exertion in *Sporobolus flexuosus* was delayed by about 2 months partially as a result of 38 mm less rainfall at one of the research sites in the study of GIBBENS (1991). This author suggested that competition for soil water among annual species and *S. flexuosus* possibly contributed to the delay in inflorescence exertion.

A wetter spring in 1984 also 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 extent of these phenological

phases in the drier 1983 and/or 1985 (fig. 2). On the other hand, low rainfall between November and February in 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 and 2).

Annual grass or dicots species

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 (fig. 3). FRESNILLO FEDORENKO et al. (1996) did not observe germination until early May in both species when rainfall during the period January-April was lower than 30 mm in central, semiarid Argentina. Germination regulation mechanisms of winter annuals thus restrict the germination of seeds to periods of comparatively abundant moisture coinciding with favourable temperature regimes (BEATLEY, 1974). Previous to germination, seeds of these species are scarified by high daily temperature oscillations at the soil surface during summer, and freezing and thawing cycles during autumn at the study site (FRESNILLO FEDORENKO et al., 1994).

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 in the season in the wetter years in *M. minima*. 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 (ARAMAYO et al., 1993).

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 by FRESNILLO FEDORENKO et al. (1996) could be attributed, at least in part, 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 plant senescence can be induced and accelerated by water stress resulting in a shorter growth cycle (ARONSON et al., 1992). Other than germination time and timing of plant death, the phenological development shown in Fig. 3 for *M. minima* and *E. cicutarium* is similar to that reported by CANO (1988), DISTEL & PELAEZ (1985) and FRESNILLO FEDORENKO et al. (1996) in these species in the Southern Caldenal. Germination and seedling establishment in *Bromus mollis* can also get started by early or mid-summer if this season is wet; this was observed for this species during the wet summers in 1984 and 1985 (figs. 1 and 3).

Woody species

Similar to results of CANO (1988) and DISTEL & PELAEZ (1985), sprouting started by early to mid spring in the woody species shown in Fig. 3. During wet summers (December 1984-January 1985 and February-March 1984: fig. 1), however, it extended until

the end of this season or even early autumn in the caducifolious (*Geoffroea decorticans*, *Lycium chilense*, *Prosopidastrum globosum*, *Prosopis alpataco*) or evergreen (*Brachyclados lycioides*, *Condalia microphylla*, *Chuquiraga erinacea*, *Larrea divaricata*, *Schinus fasciculatus*) species (fig. 3). Timing for the vegetative stage of development may thus go well beyond limits given by CANO (1988) and DISTEL & PELAEZ (1985) for these species. Low precipitation amounts have suppressed vegetative activity in *Larrea tridentata* (Sesse & Moc. ex Dc.) Cov. (SHARIFI et al., 1988). On the other hand, summer rains may trigger summer growth in this species in the Mojave Desert if the precipitation is > 25 mm (BEATLEY, 1974), which can be attributed to its lateral shallow roots in addition to its deep main root (LUDWIG, 1977). The sensitive response of lateral roots to small amounts of precipitation allows the plant to take advantage of increased moisture supply at the soil surface following precipitation. An additional active growth period in *L. tridentata* was observed in late fall (November and December) associated with an unusually warm and moist December (SHARIFI et al., 1988). It appears that *Larrea* may have the genetic potential for multiple patterns of growth, depending on climatic conditions; shifts of growth activity towards early spring or late summer can depend on favourable temperatures and the timing of precipitation (CUNNINGHAM et al., 1979). Production of vegetative structures has also been fostered by higher levels of water availability in the

desert shrubs *Jatropha cinerea* (Ortega) Muell. Arg. and *J. cuneata* Wiggins & Rollins (MAYA & ARRIAGA, 1996).

The reproductive stage has been reported to occur during spring and/or summer in these species (ARAMAYO et al., 1993; CANO, 1988; DISTEL & PELAEZ, 1985). CANO (1988) and DISTEL & PELAEZ (1985), for example, confined flowering to December in other *Prosopis* species, but the boot and flowering stages occurred during the previous 2 months in *P. alpataco* in our study (fig. 3). The reproductive stage for the species shown in Fig. 3 occurred thus at some additional times other than those given by ARAMAYO et al. (1993), CANO (1988) and DISTEL & PELAEZ (1985). Drier conditions during early spring (September and October) in 1983 (58.5 mm) may have contributed to advance the occurrence of the boot stage in *P. globosum*; boot stage, flowering and the reproductive phase of development in *L. chilense*, and the reproductive stage in *B. lycioides* when compared with the same period in 1984 (137 mm) and/or 1985 (115.6 mm) (figs. 1 and 3). This result is similar to that obtained by CARO et al. (1997) 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 desert, spiny shrub *Fouquieria diguetii* (Tiegh.) I.M. Johnstone was greater during the dry season (MAYA & ARRIAGA, 1996); these authors suggested that this species can optimize resource use 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.

Species of a desert scrub community in Mexico (e.g., *J. cinerea* and *J. cuneata*), however, have interrupted flowering and fructification by a reduction in soil moisture (MAYA & ARRIAGA, 1996). This response has also been observed 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 (GUEVARA DE LAMPE et al., 1992). Tropical trees of Costa Rica and *Tabebuia neochrysantha* A. Gentry, a deciduous forest species, have shown the same pattern (OPLER et al., 1976; REICH & BORCHERT, 1982). On the other hand, the reproductive stage in early spring was advanced in the wetter 1984 when compared to the drier 1983 in *S. fasciculatus* (fig. 3). This result compares to that in the desert tree *Bursera microphylla* A. Gray which needed a soil moisture threshold to produce flowers but it showed abundant flowering when high soil moisture was available (MAYA & ARRIAGA, 1996). ARAMAYO et al. (1993) 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 among years, they did not relate this variability to climatic variables.

Autumn initiation (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 of development during this period in 1984 in *P. globosum* (fig. 3).

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* in the drier period (figs. 1 and 3). 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 (fig. 3); lower rainfall during this period in 1983 (59.2 mm) and 1985 (28.0 mm) than in 1984 (118.5 mm) may then contribute to explain this observation (fig. 1). This result is similar to that found in *Fouquieria diguetii*, a desert perennial scrub community species, where leaf shedding occurred as soon as soil moisture decreased (MAYA & ARRIAGA, 1996). VALVERDE et al. (1993) reported that *Larrea tridentata* can reduce water loss by vertically closing its folioles, thus reducing exposure to direct solar radiation, rather than by leaf falling during periods of water stress. It has been reported, however, that increased leaf losses in *Larrea* and in other species are coincident with seasons or years of increased leaf growth and production (e.g., FIFE & NAMBIAR, 1984; COMSTOCK & EHLERINGER, 1986). Authors have suggested that this pattern would be caused by a redistribution of nutrients from old leaves to new leaves followed by the shedding of the old, nutrient-poor leaves. If this enforced redistribution were the only control on leaf shedding, however, then one would predict an increase in leaf survivorship with increased nutrient availability. In the study of LAJTHA & WHITFORD (1989), however, leaf longevity in *L. tridentata* decreased with increased nutrient availability; perhaps as resources become less limiting to foliage

production, it becomes more advantageous to maintain a relatively young leaf population with greater absolute photosynthetic potentials (LAJTHA & WHITFORD, 1989).

Overall, phenological development in *Geoffroea decorticans* is similar to that reported by MUJICA et al. (1992) in an area with a long-term mean rainfall (583 mm) higher than that at our study site (455 mm). Sprouting in this species was initiated by the end of October in 1984 and 1985 (fig. 3), a month when rainfall was similar in both years (fig. 1). However, MUJICA et al. (1992) in *G. decorticans*, DISTEL & PELAEZ (1985) in *Prosopis flexuosa* and *P. caldenia*, and CARO et al. (1997) in *P. chilensis* reported that the beginning of sprouting in these species does not appear to be influenced by rainfall. This partially could be due to the deep and extensive root system found in these species (CARO et al., 1997; FERNANDEZ et al., 1988; PELAEZ et al., 1994; TALMON & MUJICA, 1985). *Condalia microphylla*, however, is a shrub with a relatively shallow root system (PELAEZ et al., 1994), and it showed sprouting initiation by early August during 1983-1985 (fig. 3); rainfall during the previous month (July), however, had been 0.0 mm in 1983, 67.0 mm in 1984 and 112.5 mm in 1985 (fig. 1).

A species must be able to cope with extended periods of intra-seasonal drought to be successful in the environment of the Monte Phytogeographical Province. The temporal plasticity in the phenology of some of the perennial or annual grass, dicots or woody species suggests that they are well adapted to this environment. Although the phenology of the studied species was

compared for years with total annual rainfall similar to or above the long-term mean, it must be emphasized that both wetter and drier years are part of the normal, long-term weather pattern in the Monte Phytogeographical Province.

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FIGURE LEGENDS

FIGURE 1. Distribution of rainfall at the study site during 1983-1986.











FIGURE 2. Phenological stages in desirable, intermediate and undesirable perennial grasses at a site typical of rangelands in the Monte Phytogeographical Province in semiarid Argentina during 1983-1986. Phenological stages are:  seed,  germination,  sprouting, vegetative,  stem elongation,  boot stage,  flowering,  fructification (incipient, green and/or mature fruits),  seed dispersal/fruit fall,  leaf fall/senescence,  dormancy. N.D.=Not Determined.

FIGURE 3. Phenological stages in evergreen or deciduous shrubs, deciduous trees and desirable annual grasses or forbs at a site typical of rangelands in the Monte Phytogeographical Province in semiarid Argentina during 1983-1986. Meaning of shading for the different phenological stages are as in Fig. 2. N.D.= Not Determined.

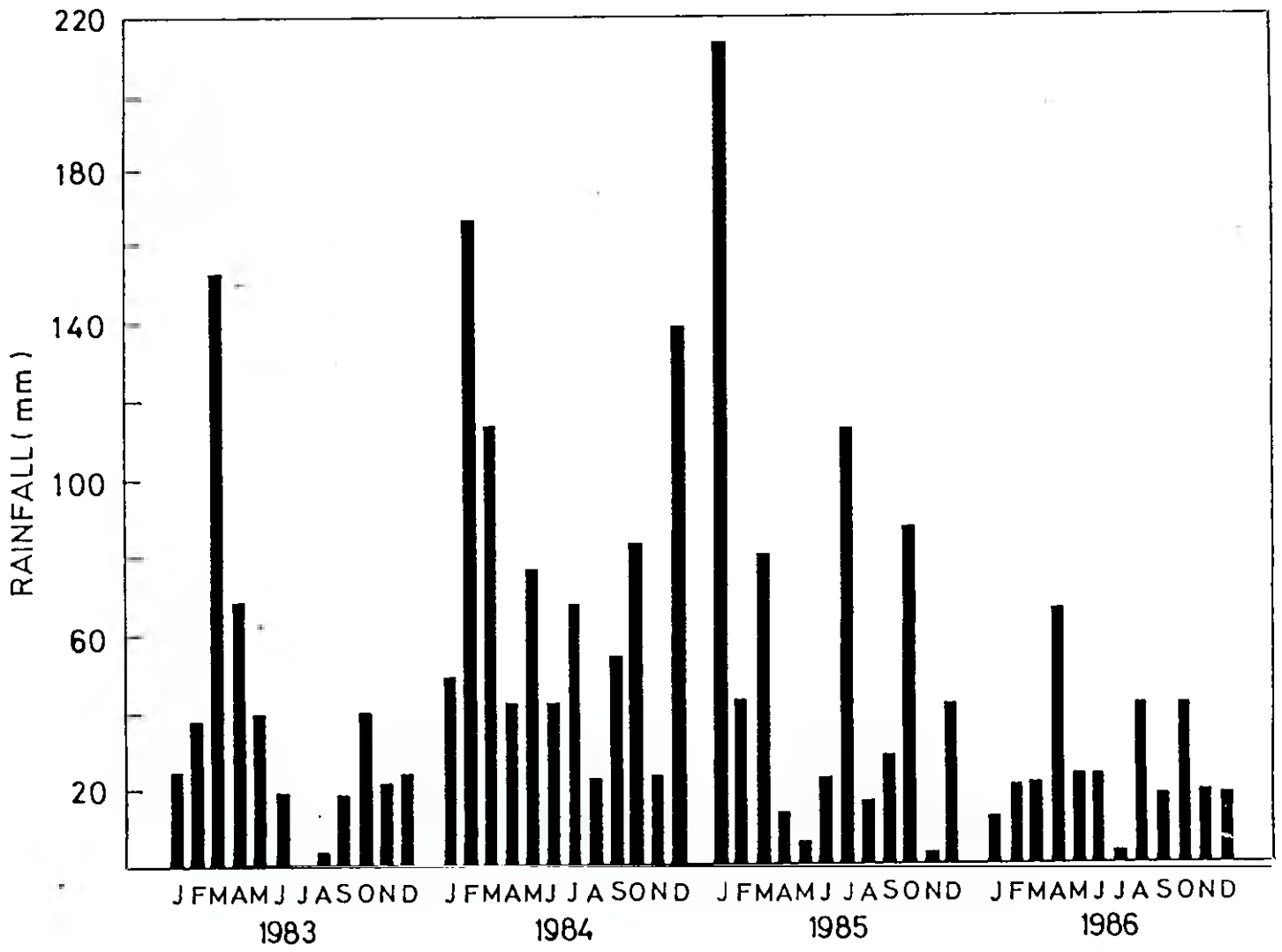
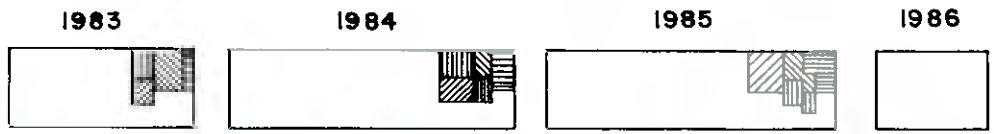


Fig. 1

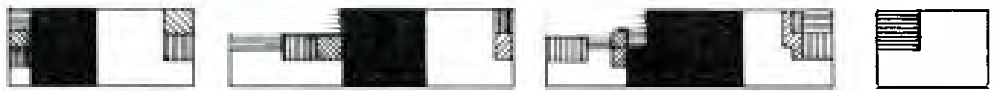
Perennial grasses

Desirable

Bromus brevis



Pappophorum subbulbosum



Piptochaetium napostaense



Poa ligularis



Sporobolus cryptandrus



Stipa clarazii



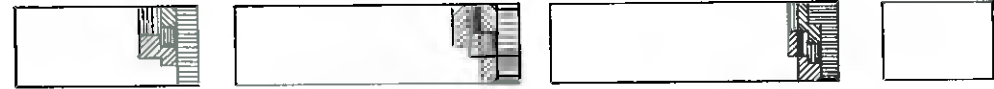
Stipa neaei



Stipa papposa

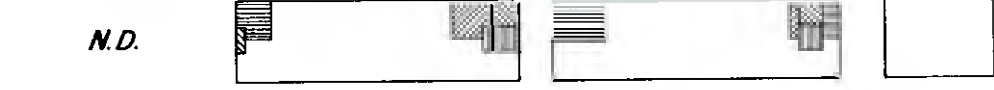


Stipa tenuis



Intermediate

Aristida pallens



Aristida spagazzinii



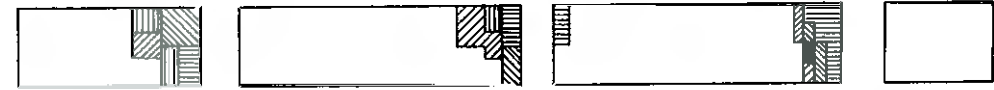
Aristida trachyantha



Melica bonariensis



Stipa speciosa



Undesirable

Stipa trichotoma



M J J A S O N D

J F M A M J J A S D N D

J F M A M J J A S O N D

J F M A M

Fig. 2

Rainfall effects on phenology of herbaceous and wood
central, semiarid Argentina

H.D. Giorgetti ⁽¹⁾, Z. Manuel ⁽¹⁾, O.A. Montenegro ⁽¹⁾, G.D.
Rodríguez ⁽¹⁾, and C.A. Busso ⁽²⁾

⁽¹⁾ *Chacra Experimental de Patagones, Ministerio de Asuntos Agrarios de la Provincia de Buenos Aires, C.C. 118, 8504-Carmen de Patagones, Argentina.*

⁽²⁾ *Departamento de Agronomía and CERZOS (CONICET), Universidad Nacional del Sur, Altos del Palihue, 8000-Bahía Blanca, Argentina; Fax 54-91-595127; email=cebusso@criba.edu.ar*

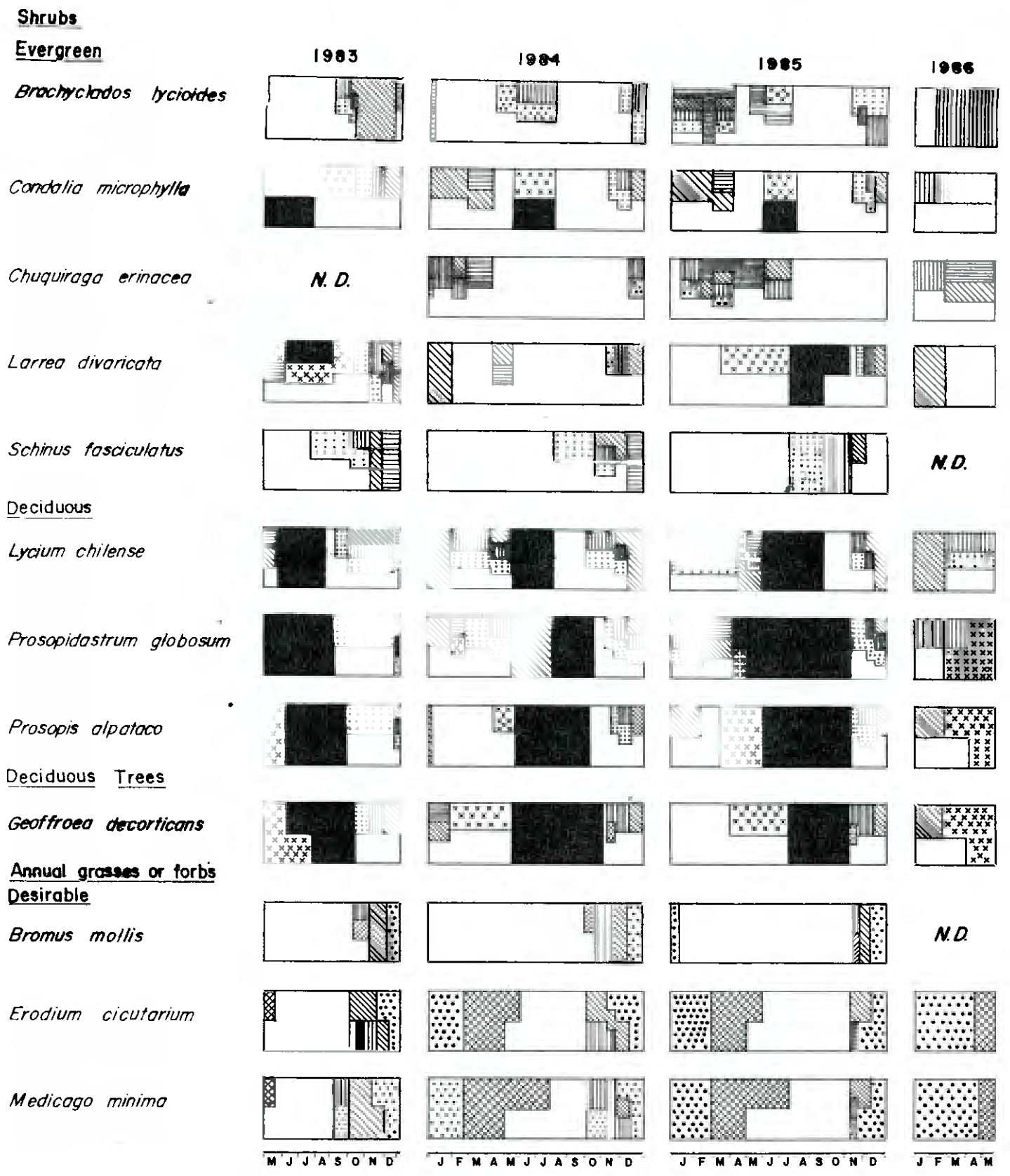


Fig. 3