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Phenology of woody plants in riverine thicket and its impact on browse availability to game species

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The study area was located in the central Free State Grassland biome, but the vegetation partially represented riparian thicket. Leaf carriage patterns of deciduous species were determined from September 2004 to August 2008. Similarities existed between *Acacia karroo* and *Diospyros lycioides* – mature leaves were present from October to April, with some dry leaves retained until June. *Ziziphus mucronata* had mature leaves from December to May with dry leaves retained until August. Mature leaves of *Searsia pyroides* were present from November to March and dry leaves until June. Though statistically non-significant, large *A. karroo* trees shed leaves faster than smaller trees. Differences were observed in phenology between years. Minimum temperature was strongly correlated with leaf phenology. Rainfall was weakly correlated with leaf phenology, though above-average rainfall resulted in increased growth of shoots and leaves. The few semi-deciduous shrubs retained mature leaves for longer periods, normally until September, and were extensively browsed. The winter-deciduous nature of woody species and absence of evergreen species have serious consequences for introduction of browsing game species on small fenced properties. The critical period, when browse was limited, is from July/August to mid-October; unless stocking rates are kept low this will necessitate the supply of feed.

Keywords: foraging ecology, leaf budding, leafless period, mixed feeder, seasonal changes, senescing leaves

Introduction

Phenology is defined as the study of the time of appearance of characteristic periodic events in the life cycles of organisms in nature (such as flowering or leafing in plants) and how these events are influenced by environmental factors (Wisiol and Hesketh 1987). Cleland et al. (2007) defined a phenophase as a particular stage of development (such as leaf budding, flowering, fruiting or leaf senescence), equivalent to 'phenological event' as it is also referred to in the literature. According to Cleland et al. (2007), global warming could alter plant phenology because temperature influences the timing of development, both on its own and through interactions with other determinants such as photoperiod (or day length).

Phenology of plants in an environment that experiences large seasonal extremes will have a profound effect on animals that feed on them, notably game species that depend on woody plants (browse). This aspect is of particular importance to the expanding game ranching industry in southern Africa, partly due to the constrained nature of game ranches because of fencing, but also due to the introduction of herbivore game species to areas outside their historical distribution range.

Distribution and habitat selection of many herbivore species is determined, among other things, by forage availability, which is influenced by habitat structure (Dörgeloh 2001). Habitat structure in the central Free State typically does not include savanna vegetation with a large diversity or concentration of woody plants. This will invariably limit the availability of food to browser and mixed-feeder game species. The vegetation that can provide the needs of these game species is restricted to riverine thickets or rocky ridges scattered through the Grassland biome. In areas dominated by winter-deciduous species and with few evergreen species present, a shortage of browse during winter months is likely to occur as the deciduous trees shed progressively more leaves. This is a common scenario on many game ranches in the central Free State, which motivated this study.

The objectives of this study were to: (1) characterise leaf phenology patterns of selected woody species in the central Free State over an extended period with variable rainfall; (2) determine if leaf phenology of *Acacia karroo* (the dominant species) differed between plants of different height classes; (3) assess temperature and rainfall as determinants of leaf phenology; and (4) determine the critical period regarding browse availability for browser game species on fenced properties where evergreen woody species are not available.

Procedure

Study area

The study was conducted on the northern part (437 ha) of the Wag-'n-Bietjie Private Nature Reserve, approximately 30 km north of Bloemfontein (28°55′ S, 26°18′ E) in the

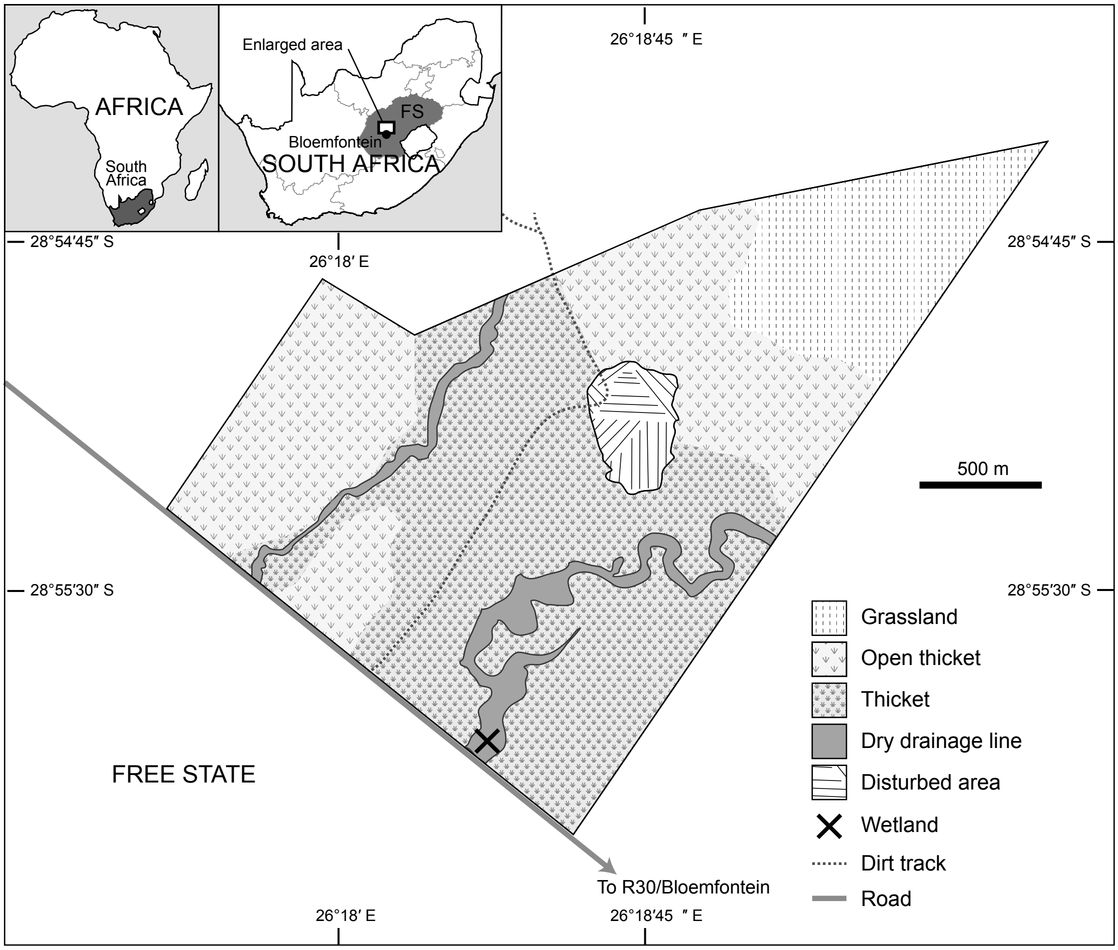

Figure 1: Location and map of the study area in the northern part of Wag-‘n-Bietjie Private Nature Reserve, South Africa. The broad area surrounding X indicates a wetland

central Free State (Figure 1). Geographically, the study area is located in the Grassland biome (Rutherford and Westfall 1994) and the vegetation of the area is described as Dry Sandy Highveld Grassland (Low and Rebelo 1996), or as Vaal-Vet Sandy Grassland (Mucina and Rutherford 2004). The vegetation is, however, more representative of *Acacia karroo* Riparian Thicket (du Preez and Bredenkamp 1991). Vegetation types (Figure 1) present in the study area, as identified and described by Janecke (2011), are: grassland; open thicket areas; dense thicket; two dry drainage lines (water courses) of the Modder River; and a disturbed area (containing ruins of buildings and a feeding site).

Alluvium outlines the area surrounding the drainage lines. Quaternary deposition underlies areas with the absence of a drainage line (Chief Director Mapping of Surveys 1998). Rock formations of the Dc13 Land Type underlying the entire area, are mudstone, shale and sandstone of the Beaufort and Ecca Groups (Land Type Survey Staff 2001). Altitude ranged from 1 335 m in the north-east to 1 286 m above sea level in the south-western part of the study area (Global Land Cover Facility 2004).

Rainfall usually occurs from October to April but is unpredictable and irregularly distributed. Mean annual rainfall for the study period, including flooding conditions, was 412 mm as measured at the Glen Weather Station approximately 20 km from the study area. During January and February of 2006 the rainfall total was 179 mm, almost half of the normal average annual total of 364 mm. The average maximum temperatures for summer and winter were 33 °C and 22 °C, respectively, and the average minimum temperatures were 16 °C and 2 °C, respectively.

The following browser and mixed-feeder game species were present in the study area at the time of study: common duiker *Sylvicapra grimmia*, eland *Tragelaphus oryx*, giraffe *Giraffa camelopardalis*, impala *Aepyceros melampus melampus* and kudu *Tragelaphus strepsiceros*. There were also an additional 13 grazing game species present.

Leaf phenology

Twenty randomly selected plants of each tree and shrub species, representing different height classes, ages and vegetation types, were marked and their GPS positions recorded. Due to the abundance of *Acacia karroo*, 20 plants from three height classes each (1–2 m, 3–4 m and >4 m) were selected and marked. Phenological leaf carriage scores of all the marked plants were recorded every fortnight

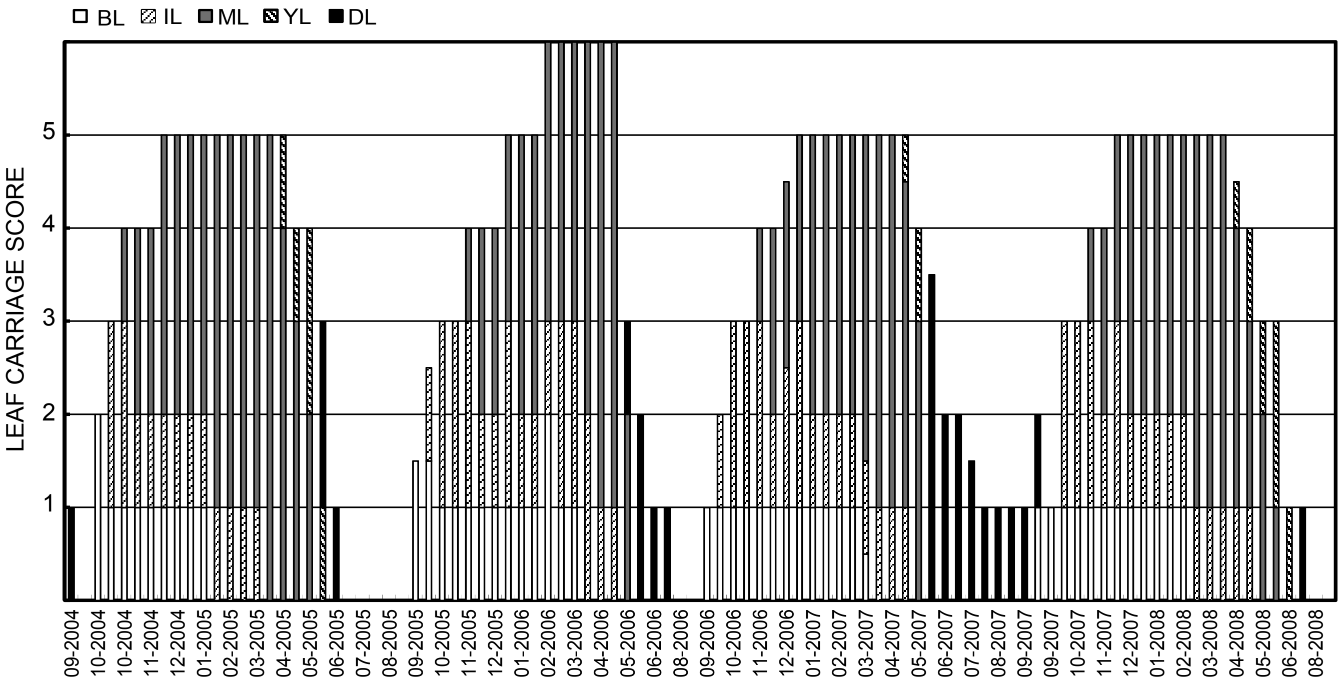

Figure 2: Leaf phenology of *Acacia karroo* trees from September 2004 to August 2008 in fortnightly intervals from the first week per month. Stack bars indicate median values per date for each phenophase of 20 marked plants in the 3–4 m height class. The *y*-axis score is explained in Procedures. BL = Budding leaves, IL = Immature leaves, ML = Mature leaves, YL = Yellow leaves, DL = Dry leaves

from September 2004 to August 2008. The following leaf carriage scores were used: 0 = no leaves; 1 = 1–15% (10%) of full leaf carriage; 2 = 16–40% (25%); 3 = 41–70% (50%); 4 = 71–90% (75%); and 5 = 90–100% (100%). During 2006 unexpected excessive late-season growth of trees and shrubs was observed after the area was flooded as a result of above-average rainfall and an additional score (class value) was added, namely 6 = 101–120%. Leaves were classified in different phenophases, namely Budding leaves (BL); Immature leaves (IL); Mature leaves (ML); Yellowing leaves (YL); and Dry, senescing leaves retained on the tree (DL). A median value for each phenophase of the 20 marked plants per species was determined per date. The sum total of these phenophase median values was calculated per woody species and indicated monthly as class values (1–6), e.g. a total score of 3 may be consisting of 1 IL + 2 ML. This was done in accordance with Dekker and Smit (1996) and Smit (2001).

Statistical analyses

Analysis of variance (ANOVA, $\alpha = 5\%$) and correlation between data sets were analysed using the statistical programme GenStat® (Payne et al. 2009). ANOVA was applied to test for differences in phenology between *Acacia karroo* trees in the various height classes (1–2 m, 3–4 m and >4 m). Year-to-year differences in median class sum totals of trees and shrubs, respectively, over the four successive years were also tested. Variables from all the data were normally distributed with homogeneous variances. Pearson's correlation coefficient was used as a measure of the linear relationship between monthly leaf carriage percentages of two species at a time. It was also applied to test the relationship between climatic variables and leaf carriage percentages of each woody species. Canonical correspondence analysis (CCA), as implemented in the CANOCO 4.5 software (ter Braak and Smilauer 2002), was used for ordination of climatic parameters and each species' phenology class totals. The Monte Carlo permutation test was applied to test for significance of the ordination data.

Results

Phenology of individual woody species

The leaf phenology of individual species did not differ significantly ($p > 0.05$, $n = 12$) between the four years of study**:** *Acacia karroo* ($p = 1.00$), *Diospyros lycioides* ($p = 0.921$), *Searsia pyroides* (syn. *Rhus pyroides*; $p = 0.969$), *Ziziphus mucronata* ($p = 0.852$), *Asparagus laricinus* ($p = 0.420$), *Lycium echinatum* ($p = 0.712$) and *L. hirsutum* ($p = 0.829$)**.**

Similarities were observed between the leaf carriage patterns of *Acacia karroo* and *Diospyros lycioides* (Figures 2 and 3), i.e. new-season leaves appeared with regularity every season during the week of 16 September, active growth ended in March, yellow leaves appeared in April (except during 2006 when leaf fall was rapid during May), and dry leaves were retained until June (except during 2007 when they were retained until leaf budding). The leafless period of *A. karroo* trees varied annually, but was roughly from July to middle September, the same period as *D. lycioides* trees. Excessive shoot growth of 20–30 cm (resulting in leaf carriage scores of 101–120%) in response to high rainfall (flooding) was observed in all the woody species during 2006. The only exception was *D. lycioides*, for which the shoots mostly did not exceed 10 cm in length. *Acacia karroo* flowers were abundant in November/December. Green pods were observed in February and retained on trees until March/April, occasionally until June when they become brown and dry. Flowering of *D. lycioides* occurred between middle October and November. The large fruits (berries) were observed between February and April and some dry fruits were retained on trees until June.

Leaf flush of *Searsia pyroides* started in the first week of October (Figure 3). The active growth period was from October to the beginning of March. It was more difficult to judge when leaves changed from immature, green leaves to mature leaves, since colour changes were subtle and leaf sizes had to be used as criteria. This gives the impression that this species has a short mature leaf phase, which might not be the case. Yellow leaves were visible at the end of March and some dry leaves (1–5%) were retained on trees from May to June. Trees were leafless from July to the beginning of October 2005, while dry leaves were retained throughout the winter of 2007 until leaf budding. Flowers were observed in November/December and fruits (drupes) between January and February. Dry fruits retained on trees were observed during May.

Leaf phenology results of *Ziziphus mucronata* (Figure 3) indicated that leaf flush usually started in the second week of October (around 15 October), but budding leaves appeared as early as 30 September during 2006. The active growth period was from October to March. This species was relatively slow to produce new leaves at the end of 2005 prior to the heavy rains of that specific summer season. The mature leaf carriage period was from December to May. Leaves usually turned yellow in May and dry leaves were mostly retained from May to July (3 months), but in 2007 the leaf retention period was from May to September and from July to August in 2008. The leafless period was from September to mid-October. *Ziziphus mucronata* flowered during summer and ripe fruits (drupes) were present on trees from March to April. Dry fruits usually had a long retention period on trees, mostly until July or occasionally just before leaf budding in spring.

Leaf carriage patterns of shrubs in general were not as distinct as those of trees. The shrubs often shed a substantial quantity of old leaves (up to 20%) during the growing season and produced new leaves shortly thereafter (Figure 4). New-season leaves of *Lycium echinatum* and *L. hirsutum* appeared in September. The end-of-season yellow leaves were visible from March to August on *L. hirsutum* and on *L. echinatum*. Leaf fall was rapid and dry leaves were not retained on shrubs for long periods. No leaves were present on *L. echinatum* between September and October of 2004 and 2005. *Lycium hirsutum* had up to 50% of its normal leaf carriage present during winter months mostly in the form of older mature leaves and some yellow leaves. Leaves produced during the excessive growth period were quickly shed and replaced with new immature leaves. The small, unobtrusive white flowers of *L. hirsutum*, which are easily overlooked, were only observed in June and those of *L. echinatum* in March and December.

The leaves of *Asparagus laricinus* are not considered to be true leaves, but rather phyllocladia – modified branches functioning as leaves (Venter and Joubert 1985), but for practical reasons they will be referred to as leaves. New-season leaves of *A. laricinus* appeared in October and end-of-season leaves turning yellow from the tips were visible from April/May to September (Figure 4). *Asparagus laricinus* was leafless by middle October 2005 just before leaf flush started, but retained some mature leaves and yellow leaves into the winters of 2006, 2007 and 2008. Unlike the *Lycium* species, *A. laricinus* retained the excessive new growth until senescence started in June 2006. Mature leaves were mostly present from November to August and yellowish leaves in an older phenological state were observed from August to September. All of the *A. laricinus* plants in a specific area of approximately 200 m^2 around the smaller drainage line (Figure 1) were leafless from 18 April to 30 May 2008, whereas this was not the case for any other plant in the rest of the study area. No obvious explanation can be offered for this phenomenon, except that soil water might have played a role. White flowers were observed on *A. laricinus* in mid-November, small, green berries in December and some red berries in February/March.

Leaf phenology of **Acacia karroo** *in different height classes*

The leaf phenology of *A. karroo* plants in the different height classes did not differ significantly (p = 0.982, n = 96) over the study period. However, despite this lack of statistical significance, differences were observed, notably smaller plants that retained their leaves for longer periods into the dry season.

Leaf phenology in relation to rainfall and temperature

Temperatures and rainfall were superimposed on phenology totals of the different plant species in the CCA ordination (Figure 5). Gradient lengths of the axes are short since associations and the influence of certain parameters on species data were tested, not gradients. The downweighting option was tested due to the high number of zero values in the data set, but proved omissible. Eigenvalues (percentage variance of the axis) were low because of all the zero values (Table 1). Cumulative species variances, indicating variance of data across the four axes, were higher for the species–climate relation than for species data, because the combined data set had fewer zero and similar values.

In contrast to the shrub species, distinct clusters of the tree species along axis 1 were evident (Figure 5). The same clusters in relation to environmental vectors were observed. Phenology data was distributed along axis 2, with *Z. mucronata* at the furthest end of the axis. *Acacia karroo* and *D. lycioides* were grouped in close proximity to each other, suggesting similarities in their leaf phenology patterns, which is confirmed by a very strong correlation (r = 0.96, p < 0.001) between their monthly leaf carriage values. Based on the results of the ordination, the phenology patterns of *S. pyroides* and *Z. mucronata* differed. *Lycium hirsutum* was grouped separately (Figure 5) due to having leaves present through most of the winter. *Lycium echinatum* and *A. laricinus* were leafless only in October 2005. A fairly strong correlation was found between *L. echinatum* and *A. laricinus* (r = 0.79, p < 0.001), which was confirmed by the ordination.

Axis 1 was associated with rainfall and axis 2 with maximum temperatures (Figure 5). Leaf phenology of

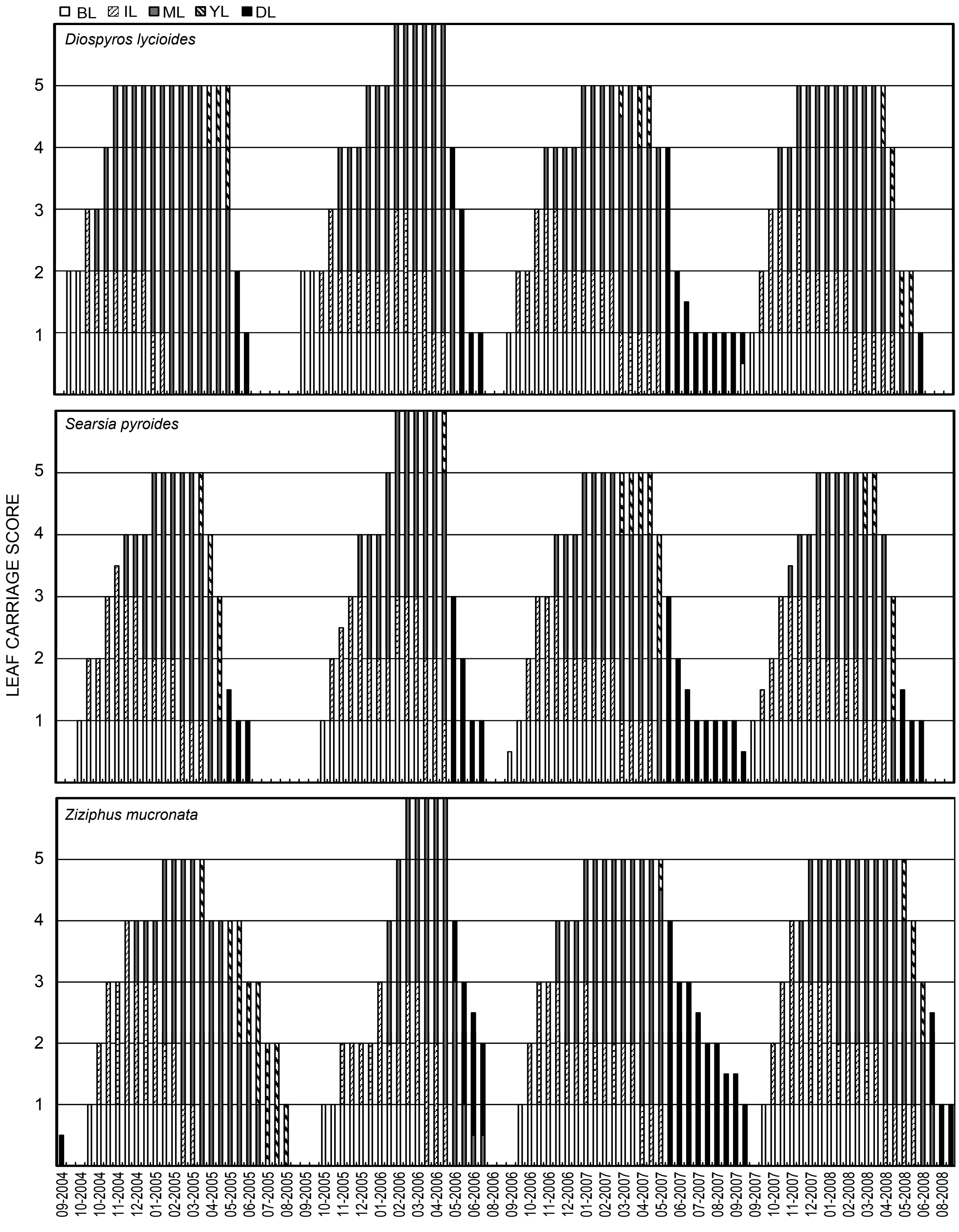

Figure 3: Leaf phenology of *Diospyros lycioides*, *Searsia pyroides* and *Ziziphus mucronata* trees from September 2004 to August 2008 in fortnightly intervals from the first week per month. BL = Budding leaves, IL = immature leaves, ML = mature leaves, YL = Yellow leaves, DL = Dry leaves

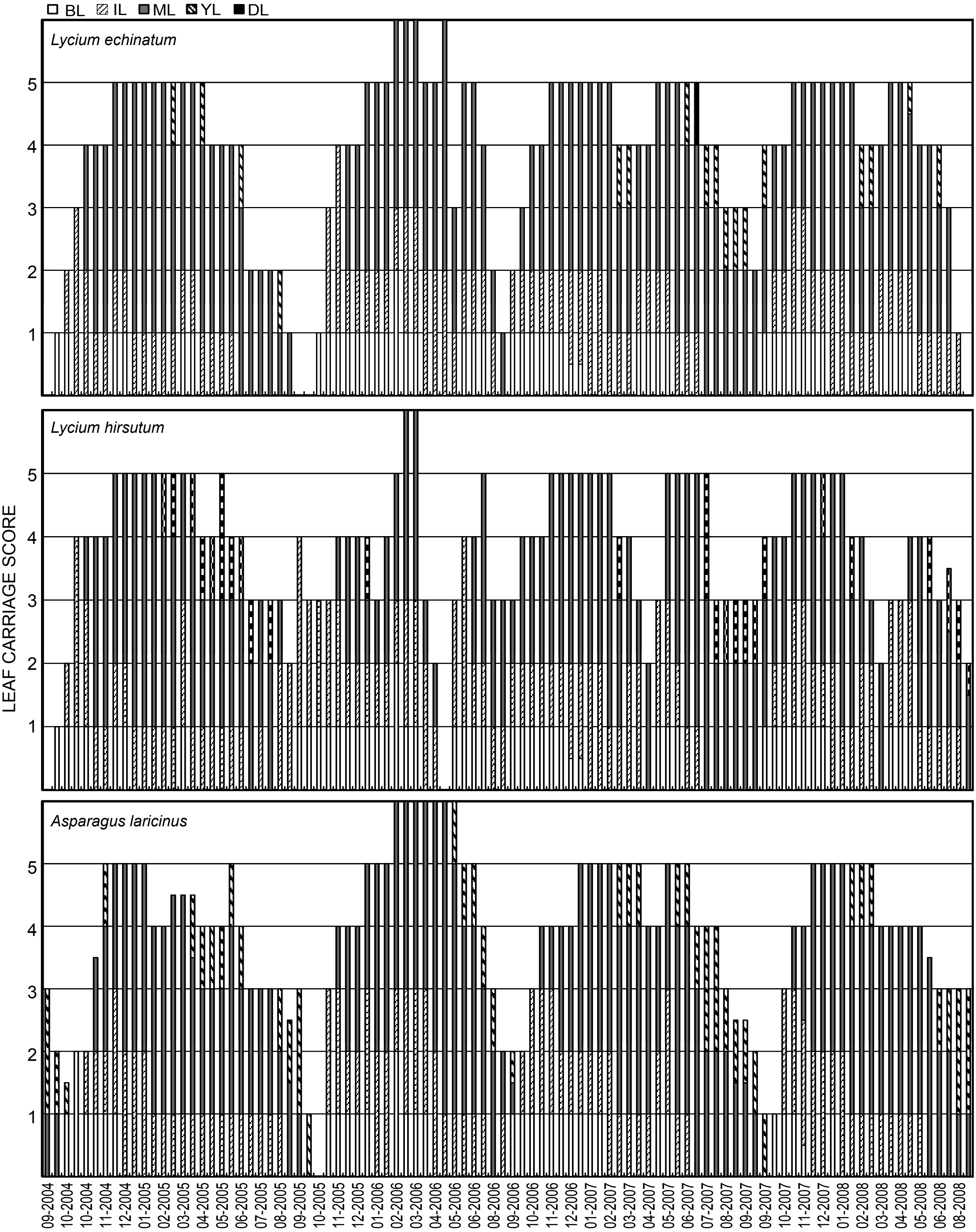

Figure 4: Leaf phenology of *Lycium echinatum*, *L. hirsutum* and *Asparagus laricinus* shrubs from September 2004 to August 2008 in fortnightly intervals from the first week per month. BL = Budding leaves, IL = Immature leaves, ML = Mature leaves, YL = Yellow leaves, DL = Dry leaves

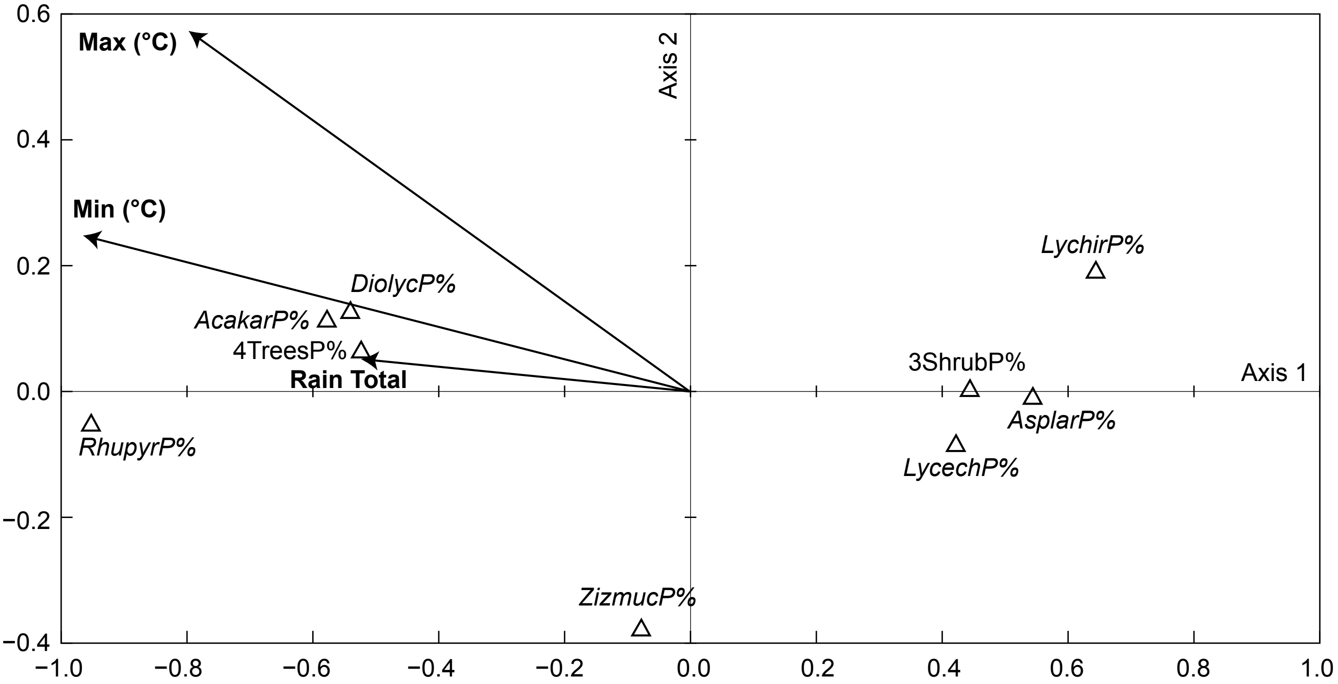

Figure 5: Canonical correspondence analysis of average percentages of phenology (P%) class value totals of each species and three climatic parameters superimposed. Median class values of the four tree species and three shrub species were also used in the ordination. Acakar = *Acacia karroo*, Asplar = *Asparagus laricinus*, Diolyc = *Diospyros lycioides*, Lycech = *Lycium echinatum*, Lychir = *Lycium hirsutum*, Rhupyr = *Searsia pyroides*, Zizmuc = *Ziziphus mucronata*, 4Trees = median values of the four tree species, 3Shrub = median values of the three shrub species

Table 1: Statistical results of the ordination data in Figure 5. Monte Carlo permutation test of the significance of the first canonical axis indicated an eigenvalue of 0.038 (*F*-ratio 21.492, *P*-value 0.0020) and of all canonical axes had a trace of 0.041 (*F*-ratio 8.075, *P*-value 0.0020)

	Axis 1	Axis 2	Axis 3	Axis 4
Eigenvalues	0.038	0.003	0	0
Species–environment correlation	0.722	0.454	0.167	0
Cumulative % variance				
of species data	32.8	35.3	35.5	70.5
of species–climate relation	92.4	99.4	100	0

A. karroo and *D. lycioides* were more strongly associated with minimum temperatures than with maximum temperatures. In contrast, leaf phenology of *Z. mucronata* and of the shrubs was poorly associated with temperatures on the ordination graph. A strong correlation ($r = 0.8$, $p < 0.001$) was found between phenology of the tree species and minimum temperatures and only a moderate correlation with maximum temperatures ($r = 0.6$, $p < 0.001$). Correlation between weekly rainfall totals and weekly phenology totals of the trees was very weak: *A. karroo* ($r = 0.087$, $p = 0.342$), *D. lycioides* ($r = 0.254$, $p = 0.108$), *S. pyroides* ($r = 0.082$, $p = 0.348$), *Z. mucronata* ($r = 0.121$, $p = 0.293$). Similar correlations of monthly totals were moderate: *A. karroo* ($r = 0.528$, $p < 0.001$), *D. lycioides* ($r = 0.458$, $p = 0.001$), *S. pyroides* ($r = 0.484$, $p < 0.001$) and *Z. mucronata* ($r = 0.326$, $p = 0.028$).

Critical period for browsers

At the end of the winter and beginning of spring the availability of browse becomes very limited in the study area due to a dominance of deciduous trees and semi-deciduous shrubs. The critical period for browsers and mixed feeders, when browse was limited, was identified as July/August to mid-October. This period includes the beginning of the spring season when woody plants sprout new leaves and ends after budding leaves have turned to immature leaves.

Discussion

Leaf carriage patterns (Figures 2 and 3) of *Acacia karroo* and *Diospyros lycioides* corresponded to some degree. The leafless period of both species varied annually, but was roughly from July to middle September (2.5 months). *Searsia pyroides* trees were leafless from July to the beginning of October 2005 (3 months). *Ziziphus mucronata*'s leafless period was from September to middle October (1.5 months) – it retained leaves for longer periods, but sprouted later than other species. No leaves were present on *Lycium echinatum* for approximately a month between September and October of 2004 and 2005 (Figure 4). *Lycium hirsutum* had up to 50% of its normal leaf carriage present during winter months. *Asparagus laricinus* was leafless by mid-October 2005 just before budding, but retained some leaves into the winters of 2006, 2007 and 2008. Although differences in tree and shrub phenology between different years were observed (Figures 2–4), it proved to be statistically non-significant ($p > 0.05$). The wettest year was 2006 (612 mm), 2008 (342 mm) was the driest, while 2004 (367 mm), 2005 (364 mm) and 2007 (362 mm) received average rainfall.

Acacia karroo is the dominant and most abundant woody species in the study area. Though no statistical differences were found between different tree heights of this species ($p > 0.05$), certain differences were noted in the field. Trees taller than 4 m shed their leaves more quickly than smaller-sized trees and no dry leaves were retained on big trees after June. These big trees also reached the immature leaf phase from budding leaves faster in the first fortnight of the season. It has been documented in other studies (e.g. Milton 1987, Novellie 1989) that young (small) trees tend to retain some leaves over the dry season, whereas mature trees generally lose most of their leaves. Recurrent growth flushes throughout the year are known to occur for saplings of several genera, while growth of mature trees is limited to one or two annual flushes (Novellie 1989). This information was unknown for *A. karroo*, not only in the study area, but also for this species in general and is of obvious importance to browse availability during the dry season. The most important implication of size differences of woody species relates to amount of browse material of large trees that is beyond the reach of smaller browser and mixed-feeder game species.

The definition of phenology emphasises the influence of environmental factors on the time of appearance of characteristic seasonal events in plants. There is very limited information available on this topic, confirmed by Darrow and Bowers (1999) and Jarzomski et al. (2000). It has been documented that other biological agents may have an influence on leaf phenology. For example, browsing by game species may induce early leaf flush (du Toit et al. 1990), while severe defoliation by insects can result in reflushing of some deciduous species within two weeks of defoliation (Bryant et al. 1991). *Colophospermum mopane* trees defoliated in February had a low leaf carriage in winter, suggesting that no reflushing occurred before the onset of the dry season, but defoliated trees produced leaf buds earlier in the growing season. This was not the case for trees that endured heavy browsing of stems and branches by elephants (de Nagy Köves Hrabar 2006). Bergström (1992) also reported that regrowth of shrub leaves after being stripped by goats was stronger during the beginning or peak of the growing season than at the end of the growing season. Though these aspects were not investigated in this study as they are considered beyond the scope of this study, their potential influence is acknowledged.

The word phenology is derived from the relationship between a periodic biological phenomenon (leaf budding, shedding, flowering, etc.) and climatic conditions, i.e. Pheno(menon) + -logy (Farlex 2011). Results of this study confirmed, as expected, that leaf phenology of all the winter-deciduous species follows the pattern of budding in spring when temperatures are rising and daylight lengths become longer, and shedding leaves in autumn when temperatures are decreasing and daylight lengths become shorter. Dry, green leaves (not brown as expected) were observed on all tree species in May of 2006 and 2007, creating the illusion of leaves still being in a green, mature state. Subzero minimum temperatures (black frost) experienced during the last week of May probably caused this. Soil temperature, soil water content, time of spring rain and amount of rainfall can also exert a secondary influence on phenology (Cleland et al. 2007). Soil properties were not measured since the potential influence of soil was deemed of lesser importance in the study area because the represented tree and shrub species often showed a strong preference for a specific soil type and not all species occurred on all the represented soil types.

During the summer rainfall season of 2006 the study area was flooded. Despite the observed excessive growth of woody plants (Figures 2–4) in response to the above-average rainfall of the 2006 season, the correlations between rainfall and leaf phenology were generally weak ($r < 0.5$, $p < 0.3$). *Acacia karroo* and *D. lycioides* started budding in the third week of September, irrespective of time of rainfall. However, *S. pyroides* and *Z. mucronata* appear to have started budding after the first spring rains, suggesting a difference between species in their response to the time and amount of rainfall. This variability is also evident from the literature. For example, Dunham (1991) reported that neither the start of leaf production of *Faidherbia albida* trees nor the duration of the leaf production period was directly related to rainfall, whereas Skarpe and Bergström (1986) and Milton (1987) observed definite responses of several woody species to rainfall. The possible interaction between rainfall and leaf budding of the plants of the study area, including additional statistical results, is presented in detail in Janecke (2011).

All the woody species present in the study area are known to be edible to browsers and mixed feeders (Kok and Opperman 1980, Buys 1990, van Wyk et al. 2000) and clear signs of browsing were observed during the study. Leaves of *Searsia pyroides* have a strong, resinous smell if bruised, but signs of browsing of this species have been observed during winter around the feeding areas. Kok and Opperman (1980) and Owen-Smith and Cooper (1985) also reported that game feed on *S. pyroides* but indications are that it is mostly utilised during periods of limited forage resources.

Availability of quality browse due to senescing leaves became progressively less from June to September (Figures 2–4), which represents one-third of the year. The end-of-season senescence proved to be more variable than springtime budding. The intensity of the critical period increases in time as trees, followed by shrubs shed their leaves until the critical period peaks in September when browsable leaves are almost absent. The critical period for browsers and mixed feeders is thus from July/August to middle October. The ‘scarcity’ of quality browse towards the end of the critical period is aggravated by the fact that budding leaves, appearing in September/October, are considered to have a higher phenolic content than immature or mature leaves, rendering them more indigestible in some tree species (Cooper 1982, Cooper et al. 1988, van Essen et al. 2002).

Animals are known to feed on pods, fruits, dry leaves and fallen leaf litter during the dry season (Kok and Opperman

1980, Owen-Smith and Cooper 1985, Buys 1990). Leaf fall was rapid and dry leaves were not retained for long periods, mostly only until June. *Ziziphus mucronata* proved to be an important species to sustain browsers during the onset of the critical period (from June to beginning of August), being the only tree species with mature and/or dry leaves. It also retained dry fruits until July, occasionally until September. *Acacia karroo* and *D. lycioides* usually retained some pods and fruits up to June.

Shrubs in the study area mostly had up to 50% of normal leaf carriage present during the critical period, in the form of older mature leaves and some yellow leaves. The shrubs, retaining mature leaves for longer periods than the trees, are also important to sustain browsers and mixed feeders in the study area for the first part of the critical period and are browsed extensively. The *Lycium* species especially were browsed down to about 1.2 m in height and about 1 m in width (Janecke 2011). In surrounding areas outside the study area, these *Lycium* species become large shrubs of 2–3 m. Most of the *Lycium* plants are present in the dry drainage lines of the study area. *Acacia karroo* is by far the most abundant species, whereas *D. lycioides*, *Z. mucronata* and *A. laricinus* seem to be evenly distributed through the different vegetation types, except in the open thicket areas where they are not in abundance. Consequently, the browsers and mixed feeders are not limited to specific vegetation types to find the palatable species. Seasonal movements of these animals in their search for browse in the confined study area are discussed in detail by Janecke (2011).

In a similar environment in the Willem Pretorius Game Reserve — but where evergreen species are present on rocky hills — the critical period is reduced and stretches from middle August to October and not the dry season as a whole (Theron 2006). From a game ranching perspective it differs from the study area in that the animals can sustain themselves on less preferred, more unpalatable evergreen species and it is thus not necessary to supply feed. In the study area, there are no other browse resources available at the end of the critical period, thus necessitating the supply of feed. In this regard the stocking rate is also very important and a conservative stocking rate is essential to lower the risk of game losses and to prevent damage to the browse resource.

Compared to studies in other geographical regions, it becomes evident that extrapolation of results cannot be done over different climatic regions. For example, Dekker and Smit (1996) reported that availability of browse in mopane bushveld in the Limpopo province was lowest from September to November and new-season leaves only appeared from middle November, which differs from results of this study. They concluded that browser and mixed-feeder game species selected different plant communities at different times of the year in order to find woody species that had longer leaf carriage periods. October is viewed as the most limiting period for impala in the Timbavati Private Nature Reserve, when browse is almost absent (Pietersen et al. 1993). This current study is important, since very little information is published on leaf phenology of deciduous woody species in the central Free State where game ranches are increasingly being established.

Conclusions

From results of this study it is clear that late dry season availability of browse is the major trophic limitation to browsing game species in a confined space such as the study area. The critical period was identified as from the end of July/beginning of August to the middle of October. *Acacia karroo*, the most abundant woody species in the study area, represents a substantial browse resource during summer months, but due to its winter-deciduous nature and the absence of evergreen species, the only available browse during the critical period is in the form of leafless shoots, a small percentage of semi-deciduous shrubs retaining end-of-season leaves, some dry leaves retained on trees, and a few tall *Searsia lancea* trees of which the lower branches were quickly stripped of all browse material. The absence of rocky ridges and other vegetation units where evergreen species such as *Olea europaea* and *Buddleja saligna* are present, aggravated the problem.

The only alternative to removing animals that are dependent on browse during the critical period, was to provide feed (lucerne and game pellets in the case of this study). It was thus not surprising that animals concentrated around feeding sites during the dry season, instead of dispersing over a wide area in search of browse. This is not a natural situation, but the consequence of the small size of the private nature reserve that limits availability of browse resources to animals. Phenology patterns of the woody plants in relation to specific seasonal rainfall and temperature patterns need to be observed and adjustments made to the feeding program as required. While the decision to introduce browser and mixed-feeder game species on small, fenced properties outside their normal distribution range is controversial, it is clear from the results of this study that managers should take cognisance of the severe limitations present in such confined spaces regarding ability of vegetation to support these game species during the identified critical period.

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