

Defoliation effects on resource allocation in Arizona cottontop (*Digitaria californica*) and Lehmann lovegrass (*Eragrostis lehmanniana*)

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Arizona cottontop (*Digitaria californica*), a bunchgrass native to the Chihuahuan and Sonoran Deserts in North America, and Lehmann lovegrass (*Eragrostis lehmanniana*), a bunchgrass introduced to the southwestern USA from southern Africa, were defoliated and examined for above- and below-ground productivity, nitrogen and phosphorus allocation, and photosynthetic potential. Stems plus sheaths from which leaf blades have been removed may be important to Lehmann lovegrass because this tissue is photosynthetically active and contains nitrogen and phosphorus reserves. After defoliation, Arizona cottontop re-established a canopy more quickly than Lehmann lovegrass but differences were due to greater numbers and growth rates of Arizona cottontop leaves. Rapid Arizona cottontop leaf growth was followed by a 50% decline in below-ground biomass. Lehmann lovegrass had a lower investment in above- and below-ground biomass, nitrogen and phosphorus per plant. Grazing tolerance associated with Lehmann lovegrass may be related to the prostrate form of regrowing leaves and a dense but shallow root system.

Digitaria californica, 'n polgras inheems aan die Chihuahuan en Sonoran woestynne in Noord Amerika, en *Eragrostis lehmanniana*, 'n polgras ingevoer na die suidwestelike VSA vanaf suidelike Afrika, was ontblaar en ondersoek vir bo- en ondergrondse produktiwiteit, stikstof en fosfor allokering en fotosintetiese potensiaal. Stingels plus skedes waarvan die blaarblaaië verwyder is, mag belangrik wees vir *E. lehmanniana* omdat hierdie weefsel fotosinteties aktief is en stikstof en fosfor reserwes bevat. Na ontblaring het *D. californica* 'n kroon vinniger hervestig as *E. lehmanniana*, maar verskille was die gevolg van groter getalle en groeitempos van *D. californica* blare. Vinnige *D. californica* blaargroei was gevolg deur 'n 50% afname in ondergrondse biomassa. *E. lehmanniana* het 'n laer inset in bo- en ondergrondse biomassa, stikstof en fosfor per plant gehad. Weitolerasie geassosieer met *E. lehmanniana* mag verband hou met die platgroeiende vorm van hergroeiende blare en 'n digte maar vlak wortelstelsel.

Additional Index words: Above- and below-ground biomass, photosynthesis, respiration, nitrogen and phosphorus quantities

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Introduction

Between 1860 and 1930, large cattle and sheep herds were stocked on south-western USA rangelands (Cox *et al.* 1983). Overstocking and drought caused a decline in perennial grass densities and livestock numbers. Because rangeland productivity could not be restored with native grasses, Lehmann lovegrass [*Eragrostis lehmanniana* (LL)], a perennial warm-season bunchgrass from southern Africa, was introduced to Arizona, USA in 1932 (Cox & Ruyle 1986). Between 1940 and 1960 the species was artificially established on 70 000 ha and in the following 20 years the species spread by seed to an additional 70 000 ha.

Populations of Arizona cottontop [*Digitaria californica* (AC)], a native perennial warm-season bunchgrass, continued to decline after the introduction and spread of LL (Cable 1979). There is speculation that AC is more palatable than LL, and preferential livestock grazing caused the replacement of AC with LL but there is no data to support this hypothesis (Cable 1976).

Observations suggest that LL spreads and AC declines

when mixed swards of these species are moderately grazed but populations are unchanged when mixed swards are heavily grazed. Under moderate stocking rates, cattle defoliate AC to 5 cm above the soil surface but only remove LL leaves; while under heavy stocking rates both grasses are defoliated to 5-cm heights. LL stems elongate rapidly in spring, remain green in summer after surface soils dry, and gradually die from top to bottom in winter and spring (Cox *et al.* 1990). AC stems also elongate rapidly in spring but remain green only in summer when surface soils are moist (Cable 1971). Thus the possibility exists that green LL stems plus sheaths contribute to photosynthetic efficiency.

After defoliation, nutrients are translocated from roots to shoots, from shoots to roots, or from shoots to new growth. Re-allocation patterns are used to assess a plant's response to grazing (McNaughton & Chapin 1985) and estimate long-term grazing effects on potential changes in species composition (Jaramillo & Detling 1988). Non-structural carbohydrate reserves are commonly used to map allocation patterns

in grasses (White 1973). Carbohydrate concentrations, however, may be a poor measure of carbon pools because grass biomass components change more rapidly than carbohydrates can be translated (Caldwell *et al.* 1981).

Increased nutrient uptake may allow defoliated plants to compensate for nutrient losses that occur when forage is removed, and shifts in allocation patterns may contribute to plant survival (McNaughton & Chapin 1985). This may be particularly true of nitrogen and phosphorus because both are important in mediating plant-herbivore interaction (White 1984).

This research was initiated to determine the response of AC and LL to defoliation. We measured above- and below-ground growth, photosynthesis and respiration in leaves and stems plus sheaths, and above- and below-ground allocation of nitrogen and phosphorus. Morphological and physiological plant responses are usually expressed as percentages or rates because only a portion of the plant is sampled. In this study we sampled the whole plant and values are expressed as totals.

Procedure

AC and LL tufts with similar basal areas were collected 80 km south of Tucson (31°46'N latitude, 110°51'W longitude) in south-eastern Arizona, USA. The collection site was representative of the Sonoran Desert mixed shrubland where LL has invaded (Cable 1976). The elevation is 1 250 m and the soil is a Comoro coarse loam, mixed, thermic, Typic Torrifluent (Richardson *et al.* 1979). Soils are recent alluvium, weathered from mixed rocks, moderately alkaline, greater than 1 m in depth and well drained.

The average annual precipitation is 450 mm and it has varied from 175–700 mm in the past 80 years (Cox *et al.* 1990). Precipitation is bimodally distributed: approximately 60% comes as rain between July and September and about 40% comes as rain or snow between October and April. May, June and September are usually dry but exceptions occur. Daytime temperatures average 30°C in summer and nighttime temperatures average 5°C in winter, but daytime maximums frequently exceed 38°C in June and nighttime minimums are below 0°C in January and February.

Tufts were separated into live and dead tillers and five unattached live tillers of a species were transplanted as a group in a single 15.5 × 61.0-cm PVC tube. All tillers were clipped to 10 cm heights after transplanting. One end of the tube contained a wooden plug with a 2-cm diameter hole to facilitate drainage. At three field sites 80% of the below-ground biomass of both species was found in a 15.5 × 50.0-cm area. Above-ground growth of plants grown in tubes was morphologically similar to field-grown plants. This was not the case with pot-grown plants.

Plants were watered every other day with 500 ml of tap water and fertilized weekly with 600 ml of Hoagland's solution. In the glasshouse, night and day temperature extremes and relative humidity were programmed to simulate summer growing conditions in the Sonoran mixed shrubland (Climatology of the United States 1982). Night and day temperature extremes ranged from 20–36°C, and night and day humidity extremes ranged from 50–90%. Quantum irradiance at the flag-leaf was 1 500 $\mu\text{E m}^{-2}\text{s}^{-1}$.

Seven days after transplanting, 2–5 leaves were present on all stems in each tube and 21 days after transplanting, stems of both species were elongating. On day 22 one-half of the plants of each species were harvested 5 cm above the growth media surface. Harvesting of this phenophase had an adverse effect on the above-ground growth of both species (Giner-Mendoza 1986; Obo 1986). The harvest height was selected because in preliminary studies we found that harvesting below 5 cm killed 40% of the LL and 55% of the AC. Defoliated and non-defoliated plants were randomly distributed in a 4-block bench arrangement. Blocks had four defoliated and four non-defoliated individuals of a species or 16 experimental units per block.

A defoliated and non-defoliated representative of AC and LL were randomly selected from each block 2, 4, 6 and 8 weeks after defoliation. A tiller with fully-expanded leaves was inserted in a 0.28-l plexiglas chamber. After photosynthesis and respiration measurements the tiller was removed, leaves were separated at the sheath and measurements were repeated for stem plus sheaths. Photosynthesis and respiration measurements were made on three separate tillers and repeated on the same stem plus sheaths after leaf removal. In preliminary studies we removed sheaths from both species and found that their presence or absence had no effect on photosynthesis or respiration.

Photosynthesis and dark respiration were measured in a closed system (Delaney & Dobrenz 1974) with an infra-red gas analyser. Ambient CO₂ was used to flush the chamber before each measurement (Delaney *et al.* 1974) and air leaving the chamber had CO₂ concentrations of 275 ± 25 $\mu\text{mol m}^{-2}\text{s}^{-1}$ (Pearce *et al.* 1967). Chamber air temperature was 25 ± 1°C during dark respiration and 28 ± 2°C during photosynthetic measurements. Apparent photosynthesis rates were measured under a light bank with a quantum irradiance of 1 160 $\mu\text{E m}^{-2}\text{s}^{-1}$. The light bank consisted of seven 500-W flood lamps submerged in a water bath to control temperature. Dark respiration was measured after lights were turned off and the plant material in the chamber was covered with a black cloth. Carbon dioxide concentrations were measured with a Beckman Model 865 (mention of a commercial product is for the reader's convenience and does not imply endorsement by the USDA Agricultural Research Service or the University of Arizona) infrared gas analyser and graphed with a Heath-Schlumberger Model SR-205 strip chart recorder. A budget dyna-pump (1/25 hp) circulated air inside the chamber.

Plant parts in the chamber and all remaining above-ground biomass were harvested at the growth media surface. Total leaf and stem plus sheath area were measured with an area meter. We used a 'one side' unit of reference for leaves and a one-half the actual surface area for stems plus sheaths (Nowak & Caldwell 1984). Photosynthesis and dark respiration were expressed using the formulas of Pearce *et al.* (1967) and Caldwell *et al.* (1981). Photosynthetic and dark respiration rates per total leaf area or stem plus sheath area were subtracted and the remainder expressed in $\text{mmol CO}_2 \text{m}^{-2}\text{s}^{-1}$ for both leaves and stems plus sheaths. When the total above-ground biomass can be harvested, it is desirable to express photosynthesis and dark respiration measurements on a whole plant basis (Wallace *et al.* 1984). This approach is desirable because it averages activity between

young and old green plant parts and does not over-estimate photosynthetic activity and under-estimate respiration activity (Wallace *et al.* 1985).

PVC tubes were split from top to bottom and the total quantity of roots and sand at 0-10, 10-20, 30-40 and 40-50-cm depths were washed over a 4-mm sieve. Total quantities of each above- and below-ground plant part were dried at 60°C for 48 h, weighed and ground to pass through a 1-mm sieve. Ground biomass was thoroughly mixed and three samples from each part were analysed for nitrogen and phosphorus using a digester and a continuous flow auto-analyser (Schuman *et al.* 1973). Mean nitrogen and phosphorus quantities were multiplied by the mass of the respective plant part and expressed on a whole plant basis.

Defoliated and non-defoliated plants were arranged in a randomized complete block design, with a 2 × 2 × 4 factorial arrangement. There were four blocks and each contained two species, two defoliation treatments and four harvest dates. An analysis of variance was performed for each above- and below-ground plant part. *F*-tests were used to determine differences among species, defoliation treatments, harvest dates and interactions. Because data from non-defoliated populations had greater variances than data from defoliated populations we separated means with a Tukey's *HSD*-test (Sokal & Rohlf 1981).

Results and Discussion

Above-ground growth

When grown under similar climatic and edaphic conditions, the total leaf area, leaf nitrogen and leaf phosphorus contents of AC exceeded those of LL by 38%, 23% and 75%, respectively (Table 1). In contrast, the total stem plus sheath area of LL exceeded that of AC by 25%.

A single defoliation to 5 cm above the growth media surface reduced the growth of both grasses during the 8-week study (Table 2). Defoliation removed 100% of the leaves and sheaths, and 90% of the stems of both species. Leaf area of a non-defoliated AC was three times greater than that of defoliated AC on weeks 2 and 4, and two times

Table 2 Above-ground characteristics of Arizona cottontop (AC) and Lehmann lovegrass (LL). Values are for both grasses at four sampling dates; they are presented in this format because the species defoliation interactions were non-significant

Plant component ¹	Treatment	
	Non-defoliated	Defoliated
Total leaf area (cm ²)	417 ^a	120 ^b
Total stem plus sheath area (cm ²)	412 ^a	55 ^b
Total leaf biomass (mg)	3261 ^a	1494 ^b
Total stem plus sheath biomass (mg)	5610 ^a	1183 ^b
Total leaf nitrogen (mg)	44 ^a	16 ^b
Total stem plus sheath nitrogen (mg)	70 ^a	13 ^b
Total leaf phosphorus (mg)	3 ^a	1 ^b
Total stem plus sheath phosphorus (mg)	5 ^a	1 ^b

¹Means within the same component followed by the same letter are not significantly different at the 99% level of probability

greater on weeks 6 and 8. Leaf area of non-defoliated LL was four times greater than that of defoliated LL on week 2, three times greater on weeks 4 and 6, and two times greater on week 8. Although above-ground area and nutrient concentrations differed between species (Table 1) and treatments, there were no differences among harvest dates because above-ground growth was highly variable between defoliated and non-defoliated plants of both species.

The contribution of different above-ground plant components to photosynthetic gains and dark respiration losses are shown for the two species at four dates after defoliation (Table 3). Photosynthetic and dark respiration rates, for each component, are multiplied by total component area and subtracted (Caldwell *et al.* 1981; Coyne & Bradford 1985). The

Table 3 Potential photosynthetic contribution of leaves and stems plus sheaths of Arizona cottontop (AC) and Lehmann lovegrass (LL) 2, 4, 6 and 8 weeks after defoliation. A negative value indicates that dark respiration losses may exceed photosynthetic gains

Plant component ¹	Species	Treatment	Sampling dates weeks after defoliation			
			2	4	6	8
		 CO ₂ (mmol m ⁻² s ⁻¹)			
Leaf	AC	Non-defoliated	35.8 ^b	49.7 ^a	46.5 ^a	6.5 ^d
		Defoliated	1.7 ^{fg}	6.4 ^{ef}	30.1 ^c	11.8 ^{de}
	LL	Non-defoliated	16.1 ^d	40.8 ^b	26.6 ^c	20.0 ^d
		Defoliated	0.6 ^{fg}	9.3 ^a	14.6 ^d	6.2 ^{df}
Stem plus sheath	AC	Non-defoliated	-3.1 ^c	-5.9 ^a	-5.2 ^a	-6.5 ^a
		Defoliated	-0.1 ^{bc}	0.0 ^a	-2.4 ^c	-2.5 ^c
	LL	Non-defoliated	10.6 ^a	10.5 ^a	13.9 ^a	2.7 ^b
		Defoliated	1.0 ^b	0.2 ^{bc}	1.5 ^b	2.0 ^b

¹Means within the same component followed by the same letter are not significantly different at the 99% level of probability

Table 1 Above-ground characteristics of Arizona cottontop (AC) and Lehmann lovegrass (LL). Values are averages from two defoliation treatments at four sampling dates; they are presented in this format because the species defoliation interactions were non-significant

Plant component ¹	Species	
	AC	LL
Total leaf area (cm ²)	330 ^a	205 ^b
Total stem plus sheath area (cm ²)	200 ^b	266 ^a
Total leaf nitrogen (mg)	34 ^a	26 ^b
Total leaf phosphorus (mg)	4 ^a	1 ^b

¹Means within the same component followed by the same letter are not significantly different at the 99% level of probability

value is expressed as the potential photosynthetic contribution and negative values suggest that dark respiration losses may exceed photosynthetic gains.

In defoliated and non-defoliated plants, the biomass, nitrogen and phosphorus investment in photosynthetic tissue differed between species. Since defoliated and non-defoliated plants of both species produce 4–6 tillers, and AC tillers produce 2–4 more leaves than LL tillers, these differences are attributed to greater numbers, area and mass of AC leaves.

During this 8-week study, LL stems plus sheaths contributed to the total photosynthetic gain while AC stems plus sheaths appeared to deplete resources (Table 3). Non-defoliated LL stems plus sheaths provide about one-third of the total photosynthetic gain and leaves provide about two-thirds, whereas, non-defoliated AC stems expend energy and may off-set leaf photosynthetic gains by 15%. During the summer growing season, however, these physiological differences may be inconsequential because total photosynthetic gains are 115 and 118 mmol CO₂ m⁻²s⁻¹, respectively, for LL and AC. Physiological differences may be important in fall, winter and spring when LL stems are green and possibly photosynthetically active and AC stems are brown and inactive. Extended stem photosynthetic activity may reduce plant dependence on stored crown and root carbohydrates during rapid growth in either spring or summer (Laude 1972).

Below-ground growth

At all depths, root biomass of defoliated and non-defoliated AC exceeded that of LL (Table 4) but differences were not always significant. AC roots are coarse and diameters vary

from 1–5 mm. Roots originate from tiller bases in groups of 2–5 and penetrate downward at vertical angles. Lateral roots are thread-like and grow to 10-cm lengths but there are few branches. The root colour is reddish-brown. LL Roots are fine and diameters vary from 0.25–1 mm. Roots totally occupy the growth media volume at 0–30 cm and growth occurs vertically and obliquely downward. Roots may extend 10 cm away from their origin before turning downward. All roots branch profusely and main laterals are 4–8 cm long. The root colour is tan.

A single defoliation reduced total root biomass of AC by 51% and that of LL by 21% (Table 4). After defoliation root biomass of both species declined at all depths but losses were most noticeable for AC at 10–50-cm depths. At 0–10-cm depths, root biomass of AC and LL declined 37% and 20%, respectively, while amounts at 10–50-cm depths declined 65% and 34%, respectively. The number of primary roots originating from the tiller base and their penetration depths were unaffected by the defoliation of AC. However, defoliation reduced the number of thread-like lateral roots by 60% and lateral root length declined from 10 to 4 cm.

Total root nitrogen was greatest in non-defoliated AC (40 mg plant⁻¹) and significantly less in defoliated AC (18 mg plant⁻¹), non-defoliated LL (18 mg plant⁻¹) and defoliated LL (13 mg plant⁻¹). In non-defoliated AC, root nitrogen quantities at all depths exceeded those in non-defoliated LL and defoliated plants of both AC and LL (Table 5).

Total root phosphorus was greatest in non-defoliated AC (2.3 mg plant⁻¹), intermediate in defoliated AC (1.0 mg plant⁻¹) and non-defoliated LL (1.3 mg plant⁻¹), and least in

Table 4 Below-ground biomass of Arizona cottontop (AC) and Lehmann lovegrass (LL) at five depths. Values are averages from four sampling dates; they are presented in this format because the species defoliation interactions were significant for each depth

Depth ¹	Species	Treatment	
		Non-defoliated mg	Defoliated mg
0–10	AC	1996 ^a	1264 ^b
	LL	822 ^c	657 ^c
10–20	AC	719 ^a	268 ^b
	LL	279 ^b	191 ^b
20–30	AC	574 ^a	203 ^b
	LL	201 ^b	144 ^b
30–40	AC	555 ^a	191 ^b
	LL	187 ^b	123 ^b
40–50	AC	448 ^a	149 ^b
	LL	214 ^b	122 ^b

¹Means within the same depth followed by the same letter are not significantly different at the 99% level of probability

Table 5 Total nitrogen quantities in below-ground biomass of Arizona cottontop (AC) and Lehmann lovegrass (LL) at five depths. Values are averages from four sampling dates; they are presented in this format because the species defoliation interactions were significant for each depth

Depth ¹	Species	Treatment	
		Non-defoliated mg	Defoliated mg
0–10	AC	18 ^a	11 ^b
	LL	8 ^c	7 ^c
10–20	AC	6 ^a	2 ^b
	LL	3 ^b	2 ^b
20–30	AC	6 ^a	2 ^b
	LL	2 ^b	1 ^b
30–40	AC	5 ^a	2 ^b
	LL	2 ^b	1 ^b
40–50	AC	5 ^a	2 ^b
	LL	3 ^b	1 ^b

¹Means within the same depth followed by the same letter are not significantly different at the 99% level of probability

Table 6 Total phosphorus quantities in below-ground biomass of Arizona cottontop (AC) and Lehmann lovegrass (LL) at five depths. Values are averages from four sampling dates; they are presented in this format because the species defoliation interactions were significant for each depth

Depth ¹	Species	Treatment	
		Non-defoliated mg	Defoliated
0-10	AC	0.92 ^a	0.70 ^a
	LL	0.45 ^b	0.39 ^b
10-20	AC	0.34 ^a	0.19 ^b
	LL	0.16 ^b	0.10 ^b
20-30	AC	0.33 ^a	0.14 ^b
	LL	0.11 ^b	0.05 ^c
30-40	AC	0.35 ^a	0.13 ^b
	LL	0.11 ^b	0.02 ^c
40-50	AC	0.33 ^a	0.12 ^b
	LL	0.15 ^b	0.02 ^c

¹Means within the same depth followed by the same letter are not significantly different at the 99% level of probability

defoliated LL (0.6 mg plant⁻¹) (Table 6). After defoliation there was a noticeable but non-significant decline in LL root biomass (Table 4) and root nitrogen (Table 5) at 10-50-cm depths, hence the expectation of a similar trend in root phosphorus (Opperman *et al.* 1970). After defoliation, phosphorus in LL roots declined dramatically at 20-50-cm depths. Our assumption that phosphorus would decline at the same rate as nitrogen was incorrect. Defoliation may have killed most LL roots below 20 cm and watering in the weeks to follow may have leached phosphorus from the dead root tissue. The coarse texture of LL roots suggests the presence of a complex of non-protein-nitrogen compounds. During decomposition lignin-nitrogen complexes degrade slowly, hence, the gradual decline in nitrogen and a rapid decline in phosphorus.

Weaver (1954) measured root distribution of non-defoliated and defoliated tall-grass species in the central USA. Roots of non-defoliated grasses were distributed throughout the soil profile (0-120 cm) while roots of defoliated grasses were concentrated near the soil surface (0-20 cm). In summers of average or above-average precipitation, shallow roots supply the water requirements of defoliated grasses but in summers of below-average precipitation, shallow root systems are unable to provide deep water, and during extended droughts defoliated grasses with deep root systems weaken and disappear.

Weaver (1954) and Nedrow (1937) found that deep-rooted grasses, such as AC, were replaced by shallow-rooted grasses, such as LL, when soil moisture conditions improved. Both authors attributed the replacement of deep-rooted species by shallow-rooted species to a gradual drying of the

soil profile. Deep-rooted bunchgrasses evolved where the soil profile was annually or seasonally saturated to 1.0-1.5 m, and where deep laterally-penetrating root systems extract soil moisture throughout the soil profile (Weaver & Darland 1949). AC exhibits these characteristics (Cable 1969; 1975; 1979). In contrast, LL has a shallow root system which extracts soil moisture near the soil surface (Opperman *et al.* 1970).

To determine forage removal effects on moisture in the soil profile, we removed all above-ground biomass at a semi-desert grassland site before the summer rains (unpub. data, USDA-ARS, Tucson, AZ). Prior to the summer rains soil moisture at 0-1.2-m depths ranged from 1.7-2.8% in plots where above-ground biomass was removed or untouched. Soil moisture was remeasured 48 h after a 55-mm storm and before leaf green-up. In plots where biomass was undisturbed soil moisture averaged 17, 17, 19, 15, 15 and 13% at 0-10, 10-20, 20-30, 30-60, 60-90 and 90-120-cm depths, respectively. Where biomass was removed, however, soil moisture averaged 15, 10, 6, 4, 2 and 2% at the respective depths. Hence our belief that continuous forage removal removes obstacles (dead standing biomass and litter) that slow water and enhance infiltration.

Continuous forage removal exposes surface soils to wind and water erosion (Bryan 1925; Hastings & Turner 1965; Cooke & Reeves 1976) and in summer surface soil temperatures increase by 3-8°C (Glendening 1942). To quantify surface soil temperature effects on AC and LL seed germination, Cox (1988) measured surface soil temperatures of burned and non-burned grasslands and germinated seed of both species under simulated field conditions (Martin-R. & Cox 1984). In saturated soils, diurnal temperature peaks at the soil surface ranged from 30 to 34°C in non-burned plots and from 33 to 45°C in burned plots. AC seed germination averaged 60% when temperatures ranged from 30 to 35°C but declined to 3% when temperatures exceeded 40°C. LL seed germination was similar to that of AC at 30-35°C but declined to 45% when temperatures exceeded 40°C. Increasing soil temperatures after the removal of dead-standing biomass and litter may partially explain AC planting failures and the successful establishment of LL.

Because LL densities have increased and AC densities have decreased, Cable (1976) hypothesized that LL was more grazing tolerant than AC. The 26% decline in LL total root biomass and the 50% decline in total AC root biomass after a single defoliation (Table 4) supports the belief that LL is more grazing tolerant. Grazing avoidance, after defoliation, may also relate to grazing tolerance. Observations suggest that multiple grazing events are limited by the growth characteristics of LL (Cox *et al.* 1990). After defoliation, LL leaves frequently elongate horizontally within the crown and beneath a coarse stubble of defoliated tillers. In contrast, AC leaves elongate above previously-defoliated tillers. Selective animal avoidance may be partially responsible for the spread of LL in Arizona (Galt *et al.* 1969) and southern Africa (Fourie & Roberts 1976).

Conclusions

Above-ground growth characteristics differ between AC and LL (Tables 1, 2 & 3) but it is difficult to determine if these

differences are responsible for the spread of LL and the decline of AC. It is obvious, however, that horizontal leaf growth beneath a stubble of coarse dead tillers is a primary function which reduces defoliation pressure on the primary source of photosynthesis and nutrient storage. The protection of above-ground regrowth and the presence of a dense but shallow root system suggest multiple survival strategies which minimize grazing events and maximize plant survival when soil moisture is limiting.

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