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Root longevity and phenology differences between two co-occurring savanna bunchgrasses with different leaf habits

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Summary

1. *Aristida stricta* and *Schizachyrium scoparium* are C_4 perennial bunchgrass species native to *Pinus palustris* savannas in the south-eastern USA. Species differences in growth rate, tissue nutrient content and distribution suggest that *A. stricta* is more stress-tolerant (*sensu* Grime) than *S. scoparium*. In addition, *A. stricta* retains leaves all year, whereas *S. scoparium* is winter deciduous. Based on these observations, we wanted to determine (1) whether root longevity was higher for *A. stricta* as compared to *S. scoparium*; and (2) whether the leaf habits of these species had consequences for seasonal patterns of root production and death.

2. Using *in situ* rhizotrons, we recorded root number and length of these species over the course of 2·5 years on flat, transparent 50 × 50 cm windows. Kaplan–Meier (product-limit) analysis was used to produce survival functions and to estimate median lifespans for the right-censored root longevity data. These survival functions were compared using log-rank χ^2 statistics, and a proportional hazards model was used to examine the effects of season and species on the survival of each cohort. Final demographic variables were analysed using ANOVA.

3. The median lifespan of *A. stricta* was 777 days whereas that of *S. scoparium* was 374 days. This significant difference in median lifespan was consistent between species for all cohorts in both years. Also, coincident with winter leaf senescence, root production nearly stopped for *S. scoparium* whereas *A. stricta* produced roots all year. This is probably due to the winter photosynthetic capacity of *A. stricta*. Root death did not exhibit any seasonal pattern in either species. A pulse of roots produced in apparent response to the 2000 drought was evident for *S. scoparium* but not for *A. stricta*. This cohort, however, rapidly died during the dormant season, probably due to the lack of winter photosynthesis in that species.

4. *Aristida stricta* and *S. scoparium* exhibited root production, death and longevity patterns that were predicted on the basis of ecological and leaf habit differences between them. These findings suggest species-specific differences in performance and element cycling in these nutrient-poor soils.

Key-words: *Aristida stricta*, bunchgrass, deciduous, evergreen, root lifespan, *Schizachyrium scoparium*

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Introduction

Long tissue lifespan, at least for leaves, is typical of species in nutrient-poor habitats (Aerts & Chapin 2000; Reich *et al.* 1992). These increased lifespans are thought to reduce nutrient losses in senesced tissues (Berendse & Aerts 1987; Vasques de Aldana & Berendse 1997; Vasques de Aldana *et al.* 1996). As root turnover is an important component of a plant's carbon budget, long root lifespans should confer the same benefits as those of leaves. However, considerably fewer data are available on root longevity (Eissenstat & Yanai 1997). Results from direct (Pregitzer *et al.* 1995; Van der Krift & Berendse 2002) and indirect (Ryser 1996; Vasques de Aldana & Berendse 1997; Vasques de Aldana *et al.* 1996) estimates of root longevity appear to support this prediction, although root longevity may not always increase with decreasing soil fertility (Hendricks *et al.* 1993). The evergreen leaf habit has been explained on the same basis as, by definition, evergreen species have

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longer leaf lifespans than deciduous species, and are more common in nutrient-poor habitats (Aerts 1995; Monk 1966). It is not known how the root longevities of evergreen species differ from those of deciduous species.

An important component of tissue longevity is the seasonal timing of tissue production and senescence, as costs and benefits may differ between seasons (Kikuzawa 1995). The seasonal differences in leaf production between deciduous and evergreen species have been well studied (Aerts 1995). However, seasonal differences in root production and death are poorly documented, and the factors that control them are not well understood (Hendrick & Pregitzer 1996; Joslin *et al.* 2001). Roots may respond to both internal controls (e.g. 'phenological programming'; Joslin *et al.* 2001) and external controls such as temperature and soil resource availability (Cote *et al.* 1998). In addition, individual root cohorts may exhibit different lifespans or different sensitivities to environmental influences (Weber & Day 1996). Understanding how these controls interact to affect root production and death is critical to an understanding of root demography.

Aristida stricta (Wiregrass) and *Schizachyrium scoparium* (Little Bluestem) are two bunchgrasses native to *Pinus palustris* (Longleaf Pine) savannas in the south-eastern USA. *Pinus palustris* savannas are fire-maintained and exhibit strong soil resource limitations due to their very sandy soils (Christensen 1988). One study reports low rates of net N mineralization from approximately 4–12 kg N ha^{-1} year^{-1} (Wilson *et al.* 1999). We have obtained similar values for our sites (J.B.W. and co-workers, unpublished results). Because the soils are very sandy, their water retention capacities are also low, with the drier sites (those with deeper sands) often exhibiting summer drought conditions even though rainfall is relatively high (1200 mm year^{-1}) and nearly aseasonal. Physiological, distributional and successional differences between *A. stricta* and *S. scoparium* suggest that *A. stricta* is better adapted to low soil resource availability. *Schizachyrium scoparium* is an early colonizer of sites with recent soil disturbance, whereas *A. stricta* does not readily colonize following a disturbance (Grelen 1962; Lemon 1949). The potential growth rate of *S. scoparium* is 468 mg g^{-1} day^{-1} and that of *A. stricta* is 327 mg g^{-1} day^{-1}; the N concentration of *S. scoparium* leaves is approximately double that of *A. stricta* in the field (J.B.W. and L.A.D., unpublished results). In addition, *A. stricta* has green leaves year-round, whereas *S. scoparium* is winter deciduous. Finally, *A. stricta* dominance tends to increase on the most nutrient-poor, xeric sites of the sandhills, although the two species often co-occur on subxeric sites (intermediate soil resource availability) where this study was conducted. These observations suggest that *A. stricta* is more stress-tolerant (*sensu* Grime 2001) than *S. scoparium*. The objective of this study was to quantify root longevity and demography patterns of these species to determine (1) whether root longevity was higher for *A. stricta* than for *S. scoparium*; and (2) whether the leaf habits of these species had consequences for their seasonal patterns of root production and death.

Materials and methods

The investigation was carried out at the Carolina Sandhills National Wildlife Refuge (CSNWR), near McBee, South Carolina, USA. An area of *c.* 30 × 30 m^2 was selected at a subxeric site. This site was selected because of the co-occurrence of both species and the ease of finding similarly sized individuals for transplant. The overstorey was dominated by *P. palustris* and four oak species (*Quercus laevis*, *Q. incana*, *Q. margaretta* and *Q. marilandica*).

Adult plants of similar size were selected inside the field plot (four plants each of *S. scoparium* and *A. stricta*; one *S. scoparium* plant died after transplant and was not replaced). On 19 February 1999 each plant was carefully excavated from the soil together with a semicylindrical soil monolith containing the root system (diameter 60 cm, depth 25 cm). The remaining soil just below the monolith was excavated to a depth of 60 cm and a PVC rhizotron (a semicylindrical root observation chamber of 60 × 60 cm; Fig. 1) was placed in the pit. The excavated soil, with the same profile orientation, was refilled to a depth of 25 cm. One Peltier-type thermocouple psychrometer (JRD Merrill Specialty Equipment, Logan, UT, USA) was placed in the centre of the chamber at 25 cm depth and covered with 5 cm soil. The plant and the soil monolith (25 cm deep) were placed immediately on top of the refilled soil and psychrometers. Care was taken to ensure the absence of gaps between the soil and the interior rhizotron surface. Because of the sandy nature of this soil, bulk density was likely to be similar inside and outside the rhizotrons. Hourly records of soil water potentials and soil temperatures at 25 cm depth were recorded using individually calibrated thermocouple psychrometers (Brown & Bartos 1982) connected to CR7 data loggers (Campbell Scientific, Logan, UT) during the experiment.

The rhizotrons contained a flat, transparent plexiglass window (60 × 60 cm) that allowed root observation (when not being observed the faces were covered with black, then white plastic, and covered with insulation to prevent light entry and reduce temperature effects). All roots visible through the observation window were traced onto transparent acetates (50 × 50 cm) for a total of 13 intervals during the 2·5-year study period (19 February 1999 to 1 October 2001). Roots appearing on each individual mapping date were considered to be part of the same cohort and were identified with different pen colours. Root death was also recorded with the respective date and cohort information. Roots were considered as dead when they started to show symptoms of decay (shrivelling, softening and/or partial decomposition) and were followed until total decomposition to confirm the observation.

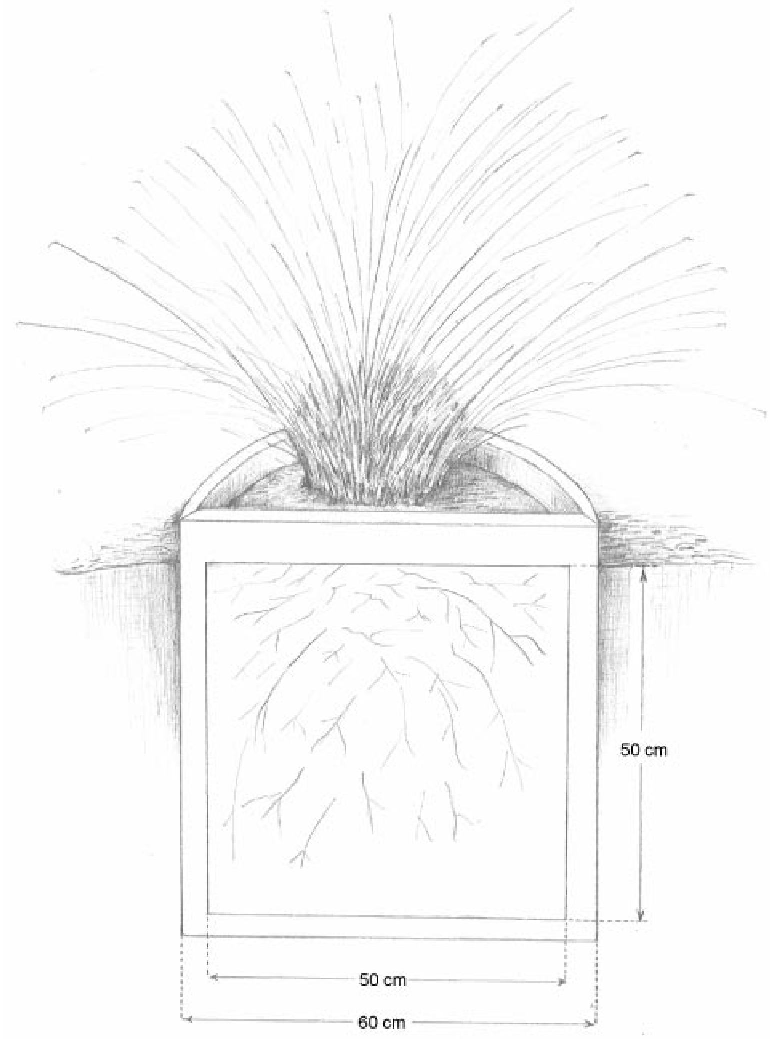

Fig. 1. Diagram of the *in situ* rhizotrons, showing the chamber with clear face exposed to indicate where roots tracings were made. When not being traced, the face was covered with white then black plastic, and the hole filled with insulation to prevent light entry and to reduce temperature effects. Psychrometers were placed in the middle of the rooting zone at 25 cm.

In March 2000 a prescribed burn crossed a fire line around the plot. Plants in five of the seven chambers were burned and two were untouched (one of each species). The fire was fast-moving and did not damage any of the observation windows. Comparisons of cohort production, growth, mortality and longevity before and after the fire, and between burned and unburned chambers, did not reveal any response to the fire (data not presented). As a result we included all chambers in the analysis, and make the assumption that the fire did not substantially alter our overall results.

ROOT SURVIVAL ANALYSIS

The numbers of live and dead roots were quantified from the traced acetates for each cohort and mapping date. Lateral roots were counted as new roots when they were longer than 2 mm. Longevities were calculated as the time between birth and death of each root. Root survival tables were constructed by calculating the number of roots for each longevity class and cohort. In survival analysis, any individual that is not followed for its entire lifetime is considered right-censored. Therefore roots that had not died by the end of the study were identified as right-censored. Root survival functions for each species were estimated via survival analysis using the Kaplan–Meier (product-limit) method for roots from all cohorts, and median lifespan values for each species and cohort were estimated (see Black *et al.* 1998 for a detailed discussion of survival analysis).

Log-rank χ^2 statistics were computed to test for homogeneity of survival functions across species (Prentice & Kalbfleisch 1979). Because we had no prior knowledge of the root survival distributions, we fitted exponential, Weibull and log-normal distributions to our data; the Weibull distribution is presented here because it provided the best fit (Black *et al.* 1998). The Weibull distribution is described by two parameters: a scale parameter, α and a shape parameter, β. The main determinant of degree of hazard and average life span is α. The shape parameter β corresponds to change in the degree of hazard over time. When $\beta = 1$, the hazard is constant and the probability of a living root surviving until the end of a given period is constant for that period. When $\beta > 1$ the risk increases with age; when $\beta < 1$ the risk decreases with age. Weibull fitting and estimation of α and β parameters were done separately for each species, seasonal cohort and year. Parameters of each survival curve were compared by the degree of overlap between the 95% confidence intervals. Unless otherwise noted, all statistical analyses were carried out using JMP STATISTICAL DISCOVERY Software (version 4·0, SAS Institute, Cary, NC, USA).

RISK ANALYSIS

A proportional hazards model (Cox 1972; Wells & Eissenstat 2001) was used to examine the effect of season on survival time. For this analysis, cohorts of each species were consolidated in two groups: spring + summer (growing season) and autumn + winter (dormant season), and analysed separately for 1999 and 2000. The growing season was defined as the period between mapping dates when all plants had green leaves; the dormant season as the period between mapping dates when the leaves of deciduous species (e.g. *S. scoparium*) had senesced. The last growing-season date for 1999 was 20 August The 2000 growing season began on 19 March and ended 28 August The 2001 growing season began on 14 March, and the final mapping date of the study was 1 October. The proportional hazards model included species effect, season effect, and a species–season interaction term. The model was fitted using a maximum-likelihood method to estimate the regression parameters associated with the explanatory variables and their standard errors. A conditional risk ratio (or hazard ratio) and its confidence limits were also computed from the parameter estimates.

Table 1. Survival analysis of roots of two sandhill perennial grass species during the study period (834 days). Data represent survival times of four root cohorts produced between spring 1999 and the end of summer 2000 (roots were tracked from 19 February 1999 until 1 October 2001)

Cohort (season/year)	Species	Number of roots			Survival analysis*				Weibull curve-fitting†		
		Dead	Censored	Total	Median days	χ^2	$P > \chi^2$	α	CI (95%)	β	CI (95%)
All											
Spring 1999–winter 2000	*A. stricta*	569	1280	1849	777	349·07	**<0·0001**	993·6	939–1057	1·77	1·65–1·90
	S. scoparium	844	586	1430	374			561·9	536–590	1·44	1·36–1·52
Spring and summer 1999	*A. stricta*	175	290	465	>834	54·67	**<0·0001**	1816·8	1501–2284	0·92	0·80–1·06
	S. scoparium	230	151	381	508			849·2	726–1008	0·82	0·73–0·92
Autumn and winter 1999	*A. stricta*	252	298	550	>707	65·67	**<0·0001**	767·3	738–802	3·41	3·04–3·81
	S. scoparium	108	20	128	438			559·3	510–615	2·04	1·72–2·39
Spring and summer 2000	*A. stricta*	77	381	458	>707	198·27	**<0·0001**	445·0	426–471	9·27	7·35–11·49
	S. scoparium	428	324	752	368			399·9	387–414	3·03	2·78–3·30
Autumn and winter 2000	*A. stricta*	65	311	376	>368	33·35	**<0·0001**	450·1	408–515	3·47	2·79–4·25
	S. scoparium	78	91	169	326			348·9	349–429	2·51	2·03–3·05

*Median lifespan was estimated by Kaplan–Meier (product-limit) survival analysis. Log-rank homogeneity test compares survival differences between the two species. Estimated median lifespan is provided with 95% confidence interval (CI). If >50% of the roots were still alive at the end of the study, (right-censored) median lifespan cannot be calculated and is expressed as greater than the study period length.

†A Weibull distribution was fitted to the survival data and the fitting parameters (α and β) estimated. Mean lifespan of the 62% percentile (α) and the magnitude of the risk slope (mortality risk, β) are listed with lower and upper 95% CI.

ROOT LENGTH DATA AND FINAL DEMOGRAPHIC VARIABLES

Roots of each date and cohort were retraced individually onto transparent acetates from the original root maps. Retraced maps were scanned individually on a flat-bed scanner (200 dpi resolution and automatic contrast) and images were saved as '.tif' files. Images were imported and analysed using DELTA-T SCAN image analysis software (Delta-T Devices Ltd, Cambridge, UK), and root lengths were estimated. In order to determine the relationships between root number and length, species-specific regressions were fitted to total live numbers and lengths at each mapping date for each individual chamber. Total root proliferation, death and percentage mortality (percentage of total death to total root proliferation) were calculated for root numbers for each species, seasonal cohort and year at the end of the experiment. Differences between species in total root proliferation, death and mortality at the end of the experiment were tested by ANOVA.

Results

Total yearly rainfall for 1999 was approximately 12% below average and 19% below average for 2000. The psychrometers showed significant soil drying during the growing seasons of both years (Fig. 2). Soil temperatures tracked the seasons with lows near 2 °C and highs around 30 °C.

These species exhibited significant differences in root longevity (Table 1; Fig. 3). Median lifespan of *A. stricta* roots (777 days) was over double that of *S. scoparium* roots (374 days). This difference in longevity was consistent for all cohorts in both years (Table 1). In addition, except for the first cohort the risk of root death for a given period increased as the roots aged for both species (β > 1 for both species, Table 1). In the first cohort β was not significantly different from 1 for *A. stricta*, but was <1 for *S. scoparium*, indicating an equal or decreasing risk of death as the roots of that cohort aged. Although the total number of roots produced was the same for both species, *S. scoparium* exhibited strong seasonality in root production for both years, whereas *A. stricta* did not (Fig. 2). There was no consistent seasonality in root death for either species.

The relationship between the total number of roots and total root length differed between each species (Fig. 4). *Schizachyrium scoparium* exhibited a significant nonlinear trend, whereas the relationship for *A. stricta* was linear. There was no statistically significant difference between species in total root proliferation or death, but all cohorts of *S. scoparium* exhibited greater mortality than those of *A. stricta* (Table 2).

Although not tested statistically, there were clear differences between the two species in seasonal production (Fig. 2). The cumulative production curves show a distinct slowing of winter production in *S. scoparium* as compared to *A. stricta*, but the same total number of roots produced over the course of the study. There were differences between species and years in the production and death of each seasonal cohort (Fig. 5). Similar numbers of roots were produced during the growing season of 1999 by each species, and they showed similar declines over time. *Schizachyrium scoparium* produced more roots than did *A. stricta* during the growing season of 2000, and those roots showed a precipitous decline (Fig. 5). These patterns are consistent with the results of the proportional hazards

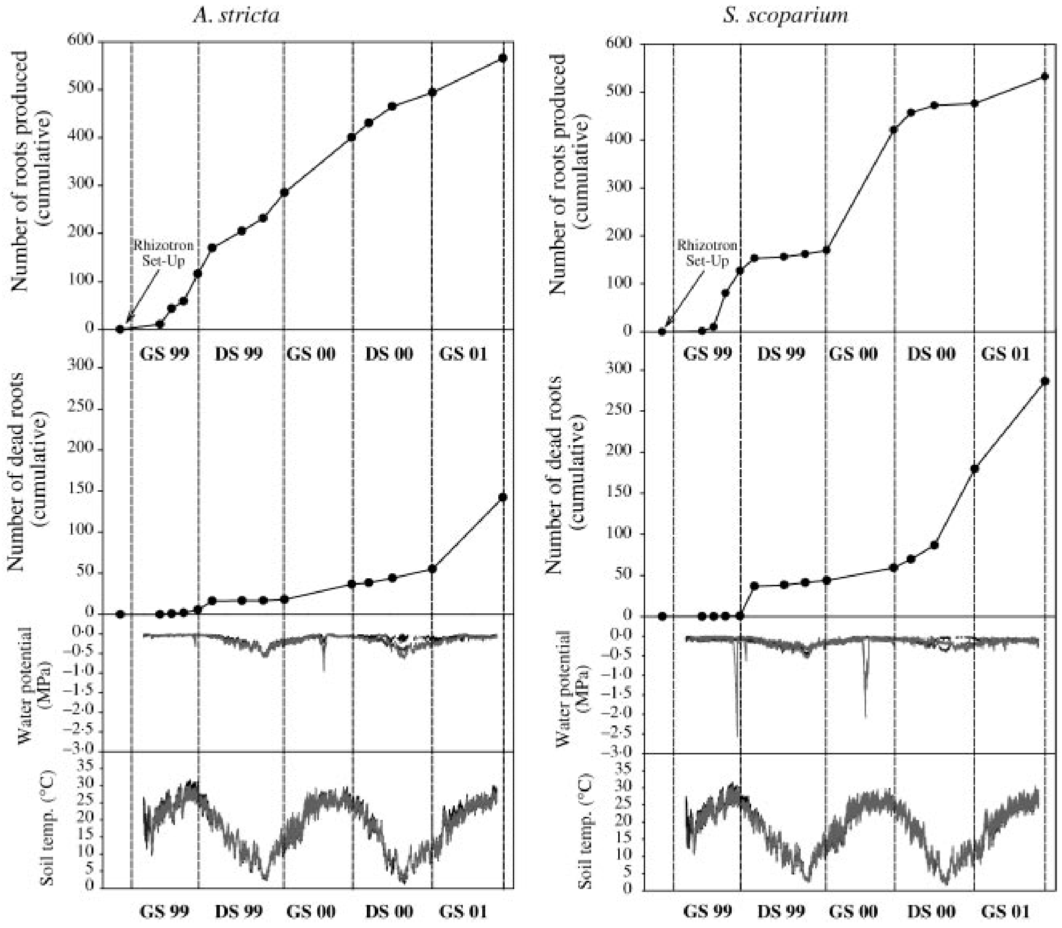

Fig. 2. Time course of root demography (total root proliferation and death) and soil water potential and temperature during the experiment (from February 1999 until October 2001; GS = growing season, DS = dormant season). Root demography data represent the mean of four and three replicate rhizotrons for *A. stricta* and *S. scoparium*, respectively, taken at 14 different mapping dates. Soil water potential and soil temperature were recorded every hour with one thermocouple psychrometer placed inside each replicate rhizotron per species. Separate curves for each psychrometer are presented.

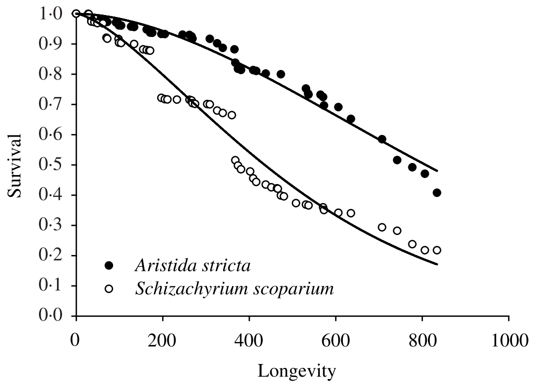

Fig. 3. Survival curves of the two grass species during the experiment, as calculated by the Kaplan–Meier (product-limit) method. Data are based on a total of 1977 roots of *A. stricta* and 1448 roots of *S. scoparium*, and the censored observations are included in the estimation of the survival probabilities. A two-factor Weibull distribution was fitted to the data to estimate the mean root lifespan for each species.

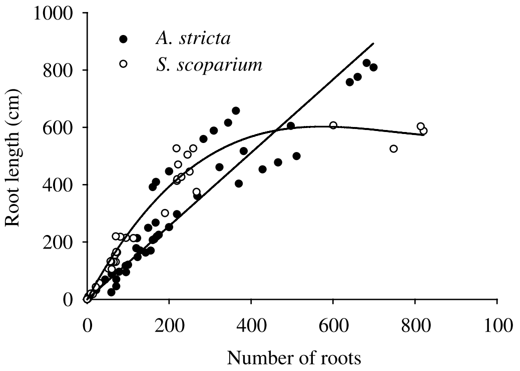

Fig. 4. Relationships between number and length of roots for each species. *Aristida stricta*: $y = 12{\cdot}78518x$ ($R^2 = 0{\cdot}950$, $P < 0{\cdot}0001$), *Schizachyrium scoparium*: $y = 26{\cdot}48412x - 0{\cdot}03737x^2 + 0{\cdot}00001659x^3$ ($R^2 = 0{\cdot}985$, $P < 0{\cdot}0001$). The models were compared using ANCOVA and represent the best fit for each species.

analysis (Table 3). In 1999 there was a significant effect of species (risk ratio = 0·66), indicating lower risk for *A. stricta* roots; and a significant effect of season (risk ratio = 1·34), indicating a higher risk of death for roots produced in the dormant season. In 2000, species and season were significant but there was also a significant species–season interaction. We interpret this interaction to be the result of a higher mortality risk for *S. scoparium* roots in the growing season of that year.

Table 2. Demography of roots of two sandhill perennial grass species during the study period (834 days): LS mean (SE) root proliferation, death, and mortality at the end of the experiment. Data are based on root counts for four successive seasonal cohorts. Species differences within each cohort were analysed by one-way ANOVA. Percentage mortality data were analysed after normalization with arcsine transformation ($n = 4$ and $n = 3$ for *A. stricta* and *S. scoparium*, respectively, df = 1,5)

Cohort (season/year)	Species	Total root production	$F_{(1,5)}$ ($P < F$)	Total root death	$F_{(1,5)}$ ($P < F$)	Final root mortality (%)	$F_{(1,5)}$ ($P < F$)
All Spring 1999–winter 2000	*A. stricta*	494 (160·4)	0·300	142 (78·7)	1·335	30·1 (4·2)	23·90
	S. scoparium	476 (185·3)	(0·9435)	281 (90·9)	(0·3001)	62·6 (4·9)	**(0·0045)**
Spring and summer 1999	*A. stricta*	116 (42·6)	0·027	43·8 (19·9)	1·169	40·6 (5·7)	9·42
	S. scoparium	127 (71·0)	(0·8752)	76·7 (23·0)	(0·3289)	67·2 (6·2)	**(0·0278)**
Autumn and winter 1999	*A. stricta*	170 (47·6)	3·045	62·5 (17·7)	1·233	39·2 (3·7)	47·78
	S. scoparium	42·7 (54·9)	(0·1414)	36·0 (13·6)	(0·3174)	81·7 (4·3)	**(0·0010)**
Spring and summer 2000	*A. stricta*	115 (79·7)	1·250	19·3 (42·9)	3·551	14·7 (3·9)	22·10
	S. scoparium	251 (92·1)	(0·3144)	143 (49·5)	(0·1182)	62·0 (12·0)	**(0·0053)**
Autumn and winter 2000	*A. stricta*	94·0 (20·6)	1·271	16·3 (6·0)	0·451	17·8 (6·6)	10·25
	S. scoparium	55·7 (28·3)	(0·3107)	25·3 (13·7)	(0·5316)	50·8 (10·6)	**(0·0239)**

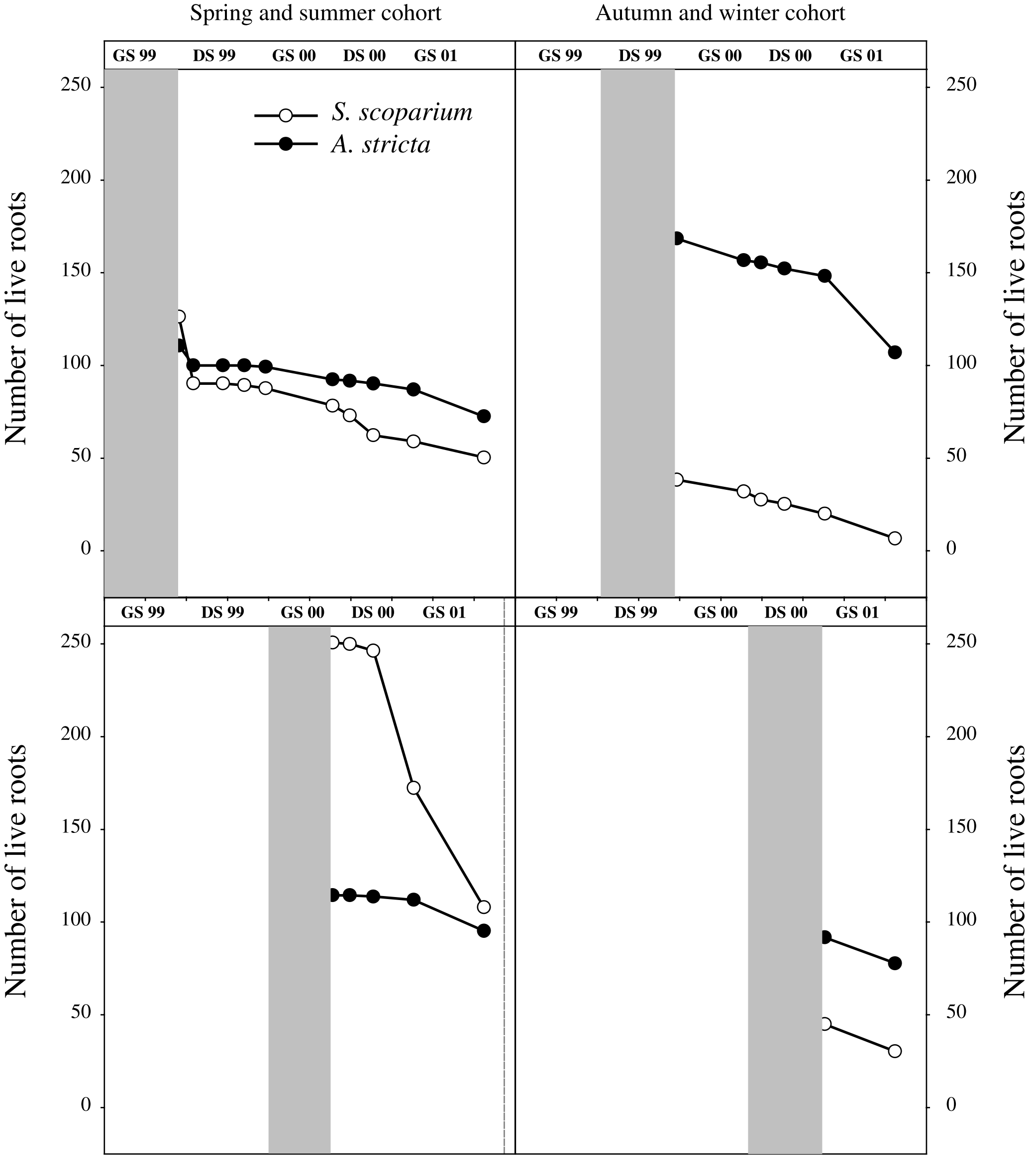

Fig. 5. Number of living roots of each seasonal cohort from the date of rhizotron installation (GS = growing season, DS = dormant season). Roots of each cohort were produced during the periods marked by shading (at the beginning of the season that cohort had zero roots).

Table 3. Results of the proportional hazards regression for root survivorship data. The analysis was used to assess the effects of three covariates (species, season and species * season interaction) on root life span. The analysis was performed separately for each year

Variable	df	Parameter estimate	SE	Wald χ^2	$P > \chi^2$	Risk ratio	CI (95%	
							Lower	Upper
1999–2000								
Species (*A. stricta*)	1	−0·41407	0·03845	106·3543	**<0·0001**	0·66096	0·61298	0·71269
Season (dormant)	1	0·29025	0·04056	49·8153	**<0·0001**	1·33676	1·23462	1·44736
Species * season	1	−0·00541	0·03838	0·01988	0·8879	0·99460	0·92253	1·07230
2000–2001								
Species (*A. stricta*)	1	−0·57079	0·05262	117·8036	**<0·0001**	0·56508	0·50971	0·62646
Season (dormant)	1	0·48924	0·05795	66·7915	**<0·0001**	1·63108	1·45595	1·82727
Species * season	1	0·15435	0·05266	8·63681	**0·0033**	1·16689	1·05247	1·29376

A method of partial likelihood estimates the β coefficient associated with each covariate in the model. A negative parameter indicates that increasing values of the covariate are associated with a decreasing risk of mortality, and vice versa for positive parameter values. A χ^2 statistic was used to test the null hypothesis that each β coefficient is equal to zero. Also reported is the risk ratio, defined as e^β. A risk ratio >1 indicates increasing risk for that variable, <1 decreasing, and =1 no difference in mortality risk. The risk ratio is interpreted as the ratio of the hazard of *A. stricta vs S. scoparium* (e.g. $\beta < 1$ indicates lower mortality risk of *A. stricta* roots); 'dormant season' (autumn and winter) *vs* 'growing season' (spring and summer); and the interaction of species by season. The significant interaction term suggests greater divergence of risk between seasons for *S. scoparium* as compared to *A. stricta*.

Discussion

Consistent with our predictions, *A. stricta* had a longer median root lifespan (777 days) than did *S. scoparium* (374 days, Table 1; Fig. 3). In a comparison of four grass species, Van der Krift & Berendse (2002) also reported longer root lifespans for slower-growing species relative to faster-growing species. The slower-growing species in that study are also those common to nutrient-poor habitats. Van der Krift & Berendse (2002) conclude that the longer root lifespans of species adapted to low-nutrient habitats represents a strategy that conserves nutrients by reducing their loss through tissue death (Aerts & Chapin 2000). Although not conclusive, our results are consistent with these ideas and support the hypothesis that *A. stricta* exhibits a suite of stress-tolerant characteristics (low relative growth rate, high nutrient-use efficiency, low rate of tissue turnover; Grime 2001). These characteristics may partially explain *A. stricta*'s dominance of the most nutrient-poor habitats of *P. palustris* savannas.

Seasonal patterns of root production also qualitatively agreed with our predictions (Fig. 2). *Aristida stricta* produced roots consistently year-round. However, *S. scoparium* showed a marked slowing of root production during the dormant seasons of both 1999 and 2000. As *S. scoparium* has no photosynthetic tissue during this season, it is likely that this pattern is explained by the lack of carbon input to supply the carbon sink that new roots represent (Farrar & Jones 2000). Because younger roots are likely to have greater nutrient-uptake capacity (Bouma *et al.* 2001), the significant winter root production by *A. stricta* may result in a seasonal advantage for this species in nutrient uptake. Winter nutrient uptake is likely in this system, given the mild temperatures and favourable soil moisture conditions. In addition, previous studies have predicted winter nutrient uptake by *A. stricta* based on seasonal tissue nutrient concentrations and biomass production (Saterson & Vitousek 1984). Interestingly, *S. scoparium* appeared to 'catch up' with *A. stricta* during the growing season by producing considerably more roots when it was photosynthesizing (Table 2). By the end of the study, this pattern resulted in essentially equal numbers of roots produced by each species. Without additional data, conclusions about the potential advantages of these alternative strategies must remain speculative. Indeed, coexisting plants can show a surprising array of growth and nutrient-use strategies (Rothstein & Zak 2001), making clear the need for more studies of whole-plant nutrient use and nutrient-foraging strategies.

Although we did not quantify root topology, the strong correlations between root number and root length reported here suggest some interesting predictions. The relationship between total length and number of roots was nonlinear for *S. scoparium*, suggesting that as its root number increased, the mean length of each root segment decreased (Fig. 4). In contrast, the trend for *A. stricta* was linear, suggesting a constant length for each root segment. As variation in segment length is associated with different topologies (Fitter 1994; Fitter *et al.* 1991), this suggests species-specific differences in architecture, with potential consequences for foraging ability.

There were apparently species-specific responses to the 2000 growing season drought, in terms of both the proliferation responses and the lifespans of the cohorts produced during that drought. Although in both 1999 and 2000 the cohort produced in the growing season had a lower risk of mortality than the dormant season cohort (Table 3), there was a significant interaction between species and season in 2000. We interpret this interaction as indicating that *S. scoparium* roots produced during that growing season were more likely to die by the end of the study period than were those of *A. stricta*. *Schizachyrium scoparium* produced a large number of roots during the 2000 growing season. These roots may have improved soil resource uptake capacity during the drought. Over half of those roots were dead by the end of our study, however (Fig. 5). Lacking experimental data, we cannot explain this pattern mechanistically. If the roots of *S. scoparium* were produced as a consequence of the drought, their high mortality during the dormant season may be the consequence of their inability to meet their respiratory costs because of the lack of winter photosynthesis. Regardless of their causes, these patterns reveal different root production and lifespan strategies that are likely to have consequences for the performance of these species in various environments, as well as plant–soil feedbacks important to ecosystem function.

In these poor quality soils, root inputs are a critical source of organic matter (Wells & Shunk 1931). At the end of the study the two species had produced nearly identical numbers of roots, but exhibited clear differences in root mortality (Table 2; Fig. 2). Mean mortality for all cohorts was approximately 30% for *A. stricta*, whereas it was 62% for *S. scoparium*. This pattern of significantly lower mortality for *A. stricta* roots existed for all cohorts in both years. Due to the low replication and high variability among replicates, the patterns in total death are not statistically significant, although the means are quite different. Given the consistently lower mortality of *A. stricta* roots, and the similar yearly total root production exhibited by both species, all else being equal (e.g. plant size, spatial distribution), soils occupied by *A. stricta* would therefore receive less total biomass input than those occupied by similarly sized individuals of *S. scoparium*. This interpretation must also be made with the caveat that equilibrium may not have been reached in the chambers. However, we consider the comparison between species to be valid, as the relative differences observed here are likely to be retained at equilibrium. Plant–soil feedbacks such as these are expected to reinforce the soil conditions to which each species is adapted (Hobbie 1992). For example, species adapted to low N availability tend to foster low N mineralization rates, and experimentation in other systems appears to support this prediction (Van der Krift & Berendse 2001; Wedin & Tilman 1990). The root biomass of *A. stricta* has higher C : N ratios (J.B.W. and L.A.D., unpublished results) than that of *S. scoparium*. As organic matter with high C : N ratios tends to foster low rates of N mineralization (Nicolardot *et al.* 2001), the low biomass inputs of low quality *A. stricta* would therefore be predicted to foster lower rates of N mineralization relative to *S. scoparium*. Experiments designed to test this hypothesis in this system are under way.

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