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CHANGES IN TILLERING DYNAMICS OF INTERCROPPED BLACK OAT AND ANNUAL RYEGRASS ENSURE A STABLE SWARD

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SUMMARY

Mixing species with different tillering peaks may enhance pasture stability, but intercropping may also alter the plants' tillering patterns. This study aimed to evaluate tillering dynamics in black oat (*Avena strigosa* Schreb.*)* and annual ryegrass (*Lolium multiflorum* Lam.) pastures grown as monocultures or intercropped. Three following treatments are established: black oat and annual ryegrass pastures grown as monocultures and an intercrop composed of these two species. Tillering dynamics were measured for black oat and annual ryegrass populations separately. When intercropped, tiller birth rates of black oat decreased (20.0 vs. 28.9 tillers 100 tillers^{-1}) and those of annual ryegrass increased (30.5 vs. 14.3 tillers 100 tillers^{-1}), compared to their monocultures. Tiller death rates for annual ryegrass did not differ between monoculture and intercropping (23.9 tillers 100 tillers^{-1}), but black oat presented higher mortality in monocultures (48.8 vs. 36.4 tillers 100 tillers^{-1}). The black oat monoculture had the lowest population stability index (0.80), whereas annual ryegrass in monoculture and intercropped pastures exhibited greater values (on average, 0.92). Our results indicated that black oat and annual ryegrass present distinct tillering dynamics whether grown as monoculture or intercropped, and suggest that intercropping species with elevated death rates (black oat) with later species (annual ryegrass) could be an important tool for maintaining pasture stability throughout the growing season.

INTRODUCTION

Maintenance of pasture persistence and productive capacity is influenced by the ability to maintain tiller population density (TPD) over time (Matthew *et al.*, 2000). In fact, in terms of tiller population, each tiller would need to produce only one new tiller throughout its life to maintain a stable pasture. However, instantaneous evaluations of TPD have not been effective in predicting the vigour and longevity of grass pastures under defoliation regimes (Bahmani *et al.*, 2003; Sbrissia *et al.*, 2010). It occurs because sporadic adjustment in TPD, as a result of phenological stage, climatic variation and management (Matthew *et al.*, 2000; Sbrissia *et al.*, 2010), is the most effective mechanism for adjusting the leaf area index (LAI) of the plant canopy (Matthew *et al.*, 2000). In this sense, tillering dynamics have an important

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role in maintaining LAI (Chapman and Lemaire, 1993) and, consequently, the productive capacity of a pasture under different environmental and management conditions.

The quality of light that reaches the auxiliary buds strongly influences the tillering process (Gautier *et al.*, 1999). In pastures subjected to intermittent stocking, changes in the canopy structure because of rapid defoliation (usually in less than five-day periods) allow a greater red:far-red ratio to reach the plant base (Ballaré *et al.*, 1992). As a result, an increase in the tiller birth rate occurs (Casal *et al.*, 1985; Gautier *et al.*, 1999), increasing TPD at the beginning of the regrowth period, with a subsequent decrease (Kays and Harper, 1974). This occurs because young tillers provide little contribution to the emergence of new tillers (Langer, 1956) and are more susceptible to shading (Ong *et al.*, 1978), with a greater chance of death before generating a new tiller. These variations in tiller birth and death rates resulting from their morphology and environmental variation are not necessarily indicators of vigour or persistence losses because they may be associated with increases in the size of the remaining tillers and, consequently, with the maintenance of LAI values (Matthew *et al.*, 1995).

Therefore, evaluation of demography and tillering dynamics, i.e. how TPD varies by changes in tiller birth and death rates, are important tools to differentiate tiller size/density compensation and transitory or permanent instabilities of the pastures. Thus, it is prudent that tiller birth and death rates be interpreted in an integrated manner because high tiller birth rates cannot be directly associated with the maintenance of pasture stability. In this sense, Bahmani *et al.* (2003), studying perennial ryegrass (*Lolium perenne* L.) under different management methods, introduced the concept of the population stability index (PSI), which seeks, from an integration of tiller birth and survival rates approach, to demonstrate possible fluctuations in pasture stability over time.

However, it is important to note that the experiments cited above evaluated pastures cultivated as monocultures and little efforts have been made to understand population dynamics in multi-specific, or intercropped, pastures. This necessity is endorsed by the positive effect of more diverse pastures on multifunctionality (Pasari *et al.*, 2013), including productivity benefits for animal production systems (Pembleton *et al.*, 2015). In this way, understanding the influences of one species on another in their population dynamics can help in choosing which species to mix, and the management systems to be adopted so that mixtures persist, maximizing the benefits of multi-specific pastures.

Based on the above, this study aimed to test whether (1) two grass species could exhibit different demographic and tillering patterns when cultivated as monocultures or intercropped; and (2) these alterations and the combined effect of tillering patterns of both species are responsible for contributing to the maintenance of population stability of the intercropped pasture.

Thus, the objective of this study was to evaluate the tillering dynamics of black oat and annual ryegrass cultivated as monocultures or intercropped throughout the growing season, as well as the effect of tillering dynamics on population stability in monocultures and intercropped pastures.

MATERIAL AND METHODS

Locality

This experiment was conducted at the Center of Agriculture and Veterinary Sciences (Centro de Ciências Agroveterinárias – CAV) at Santa Catarina State University (Universidade do Estado de Santa Catarina – UDESC), located in Lages, Santa Catarina, Brazil (27°47′S, 50°18′W, Altitude: 960 m above sea level). The soil at the experimental area is a clay Inceptisol (Haplumbrept) with a moderate A horizon (Cambissolo Húmico Alumínico Laptico). Based on a soil analysis conducted on April 6, 2011, a corrective fertilization for phosphorus and potassium was performed, according to the Fertilization and Liming Manual for the States of Rio Grande do Sul and Santa Catarina, Brazil (Soil Chemistry and Fertility Committee – RS/SC, 2004). In addition, two nitrogen (N) applications were performed using urea: the first application was on June 7, 2011 with 100 kg N ha^{-1} and the second was on August 22, 2011 with 50 kg N ha^{-1} (arrows in Figures 2 and 3; for more details about soil fertility conditions and the performed fertilizations see Duchini *et al.*, 2014). According to the Köppen classification, the regional climate is Cfb (humid subtropical) with a severe winter and mild summer, with well-distributed rainfall throughout the year (Alvares *et al.*, 2013). During the experimental year, the minimum, average and maximum-recorded temperatures were close to the historical means, and the pluviometric indexes recorded from May to October were not lower than the historical mean, with values between 121.9 and 373.0 mm month^{-1} (Figure 1).

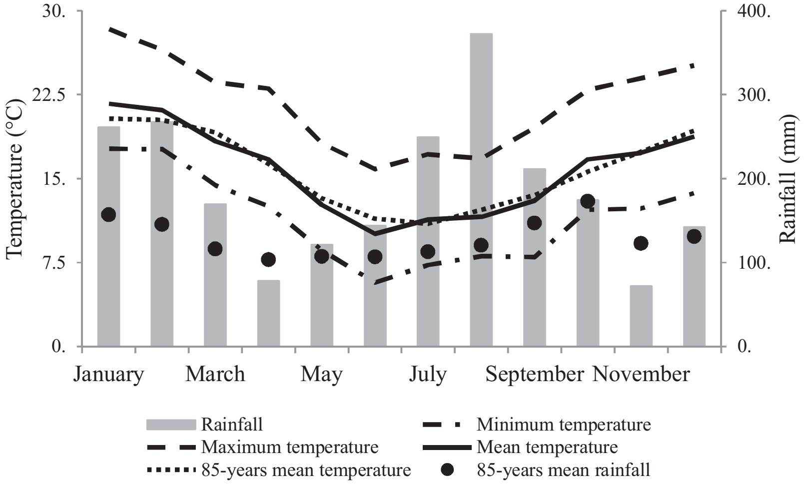

Figure 1. Rainfall and temperatures (maximum, mean, and minimum) throughout the experimental year (2011) and mean values for the last 85 years in Lages, SC, Brazil. Source: Empresa de Pesquisa Agropecuária e Extensão Rural de Santa Catarina – EPAGRI.

Treatments and experimental design

The three treatments used were black oat (*Avena strigosa* Schreb. 'IAPAR-61') and annual ryegrass (*Lolium multiflorum* Lam. 'Comum') as monoculture pastures and intercropped pastures of both species (monoculture and intercrop were considered different cultivation methods). Soil preparation was made passing the disc plough twice, the first at 20 cm depth before sowing and the second superficial (just to cover the seeds) after broadcast sowing, performed on April 20, 2011 at seeding rates of 100 kg ha^{-1} for black oat pastures, 50 kg ha^{-1} for annual ryegrass pastures, and 120 kg ha^{-1} for the intercropped pastures (90 kg of black oat seeds and 30 kg of annual ryegrass seeds). The quantity of seeds used was higher than those recommended (Santos *et al.*, 2009), to permit the maximum plant stand in all treatments, because self-thinning mechanisms control the maximum population density supported in a given environment (Matthew *et al.*, 1995). The three treatments were distributed in a completely randomized block design, four replications totalling 12 experimental units (paddocks) with an area of 98 m^2 each, separated by 1 m wide corridors.

Management

The pastures were managed under an intermittent stocking method with pre-grazing heights of 23, 17 and 20 cm for black oat, annual ryegrass and intercropped pastures, respectively. The pre-grazing height used for annual ryegrass was determined based on previous experiments, which indicated an elevated stem elongation rate starting from 18 cm (Santos *et al.*, 2016). For black oat, because of a lack of information, height was determined by plant structure, which is slightly taller compared to annual ryegrass, generating an intermediate height between both species for the intercropped pastures. The swards were reduced by 40% from the initial height (a defoliation severity that maximizes herbage intake rate by cattle; Fonseca *et al.*, 2012) in approximately 45 min by three non-pregnant Holstein heifers (15 ± 2 months old) with an initial body weight of 300 ± 20 kg. Before grazing, animals were fitted with excreta bag collectors to avoid faeces and urine influencing pasture growth. Grazing events are indicated in italicized letters in Figure 2. Pre- and post-grazing heights were monitored using a sward stick in 50 points randomly selected per paddock. Because of weed invasion during the establishment period, mainly turnip (*Raphanus sativus* L.) and bitter dock (*Rumex obtusifolius* L.), 2,4-D (dichlorophenoxyacetic acid) was applied to all paddocks at 806 g ha^{-1}.

Measurements of tiller population dynamics

Tiller population dynamics were evaluated in three PVC rings with 10 cm diameter (0.00785 m^2) per paddock fixed by metal clamps on sites with the representative average canopy conditions before the first grazing which occurred between July 13 and 17 for all treatments. The height of the PVC rings was no more than 1.5 cm and the animals were able to graze the herbage inside them. The first evaluation was performed before the first grazing, with all tillers present inside the rings, cohort *a*, marked with distinct colourful plastic clips for each species. In each subsequent evaluation, always before grazing, new colours were used to identify new tillers. This procedure was used to make it possible to recognize which species (for intercropping) and cohort each tiller belonged to. The evaluations were always performed before grazing to minimize possible differences in TPD due to grazing. Along with counting the emerging tillers, dead tillers were also counted for each species and cohort, and their identification clip was removed. Data collection ended after the last grazing event, which occurred between October 17 and 31 for all treatments.

Using these data, relative tiller birth and death rates and probabilities of tiller survival rates were calculated for each treatment and each species of the intercropped pastures according to Bahmani *et al.* (2003). For determining the tiller birth rate, all tillers that emerged between two grazings were counted and relative tiller birth rates (TBR; tillers 100 tiller^{-1}) were calculated compared to the total of existing tillers in the last evaluation. Relative tiller death rates (TDR; tillers 100 tiller^{-1}) were calculated by the same procedure, but using the number of tillers that died in the same period. Probabilities of tiller survival rates (TSR; tillers 100 tiller^{-1}) were determined by subtracting the relative tiller death rates from 1.

Based on tiller birth and survival rates, the population stability index (PSI) was calculated. This index provides an overview of the pasture tiller population stability between two successive evaluations, where values equal to or greater than 1 indicate stable pastures, and values below 1 indicate permanent or temporary population instabilities. To calculate PSI, we used an equation adapted from Matthew and Sackville-Hamilton (2011):

$$\text{PSI} = \text{TBR}_n + \text{TSR}_n$$

where PSI is the proportion of the population of tillers existing in the current evaluation and the population existing in the previous one, and TBR_n and TSR_n are the averages of relative tiller birth rates and probabilities of tiller survival rates, respectively, from n cohort existing at the current evaluation. According to this equation, if a pasture with 5000 tillers m^{-2} presents an increment of 500 tillers (i.e. 10%) between two consecutive evaluations, then the value of PSI for this period would be 1.1.

Statistical analysis

To permit simultaneous comparisons between treatments (with similar climatic conditions), TBR, TDR, TSR and PSI of each evaluation period (intervals between grazing events) were interpolated and grouped by month because grazing events occurred at distinct times (Figure 2). Following interpolation, field data were submitted to an analysis of variance using the MIXED procedure (mixed models) of the SAS® (*Statistical Analysis System*) statistical package, version 9.2. To select the covariance matrix that best suited the dataset, Akaike Information Criteria (AIC) was used. For the models, the treatment, month and block, as well as the treatment × month interaction, were used, considering repeated measurements in time (months). Means were estimated using the LSMEANS procedure, and the differences between them were determined by the probability of difference method (PDIFF), using the Student's *t*-test at a 5% significance level.

Table 1. Tiller birth and death rates of black oat (*Avena strigosa* Schreb. 'IAPAR-61') and annual ryegrass (*Lolium multiflorum* Lam. 'Comum') tillers grown as monocultures or intercropped, and the population stability indexes of these pastures over their monthly usage.

	Months				
Treatment	July	August	September	October	Mean
	Tiller birth rates (tillers 100 tillers^{-1})				
Black oat	7.4	33.6	41.8	33.0	28.9^{a}
Annual ryegrass	6.9	12.3	23.6	14.4	14.3^{b}
Black oat intercropped	4.3	23.1	35.0	17.7	20.0^{b}
Annual ryegrass intercropped	30.0	31.7	41.2	18.9	30.5^{a}
Mean	12.2^{C}	25.2^{B}	35.4^{A}	21.0^{B}	
	Tiller death rates (tillers 100 tillers^{-1})				Mean
Black oat	33.1	48.8	57.3	55.8	48.8^{a}
Annual ryegrass	9.9	18.4	28.7	34.6	22.9^{c}
Black oat intercropped	16.2	39.2	43.3	46.9	36.4^{b}
Annual ryegrass intercropped	10.6	21.0	27.5	40.5	24.9^{c}
Mean	17.5^{D}	31.8^{C}	39.2^{B}	44.5^{A}	
	Population stability index				
Black oat pastures	0.74	0.85	0.84	0.78	0.80^{b}
Annual ryegrass pastures	0.97	0.94	0.95	0.80	0.91^{a}
Intercropped pastures	0.95	0.96	1.03	0.75	0.92^{a}
Mean	0.89^{A}	0.91^{A}	0.94^{A}	0.78^{B}	

For each variable, means followed by the same upper case letter in rows and lower case in columns are not significantly different ($p > 0.05$). Standard error of the mean equals to 2.5, 1.6 and 0.020 for birth rates ($n = 62$), death rates ($n = 62$) and population stability index ($n = 46$), respectively.

RESULTS

Relative tiller birth and death rates and population stability index

The TBR increased from July to September, and decreased in October (Table 1). Regarding the monocultures, TBR of black oat was twice as high as annual ryegrass. However, when intercropped, this behaviour was inverted, with annual ryegrass exhibiting 1.5 times the TBR of those recorded for black oat.

The lowest TDR were recorded during July, with an increase until October, when the highest monthly value was observed (Table 1). Black oat tillers presented the highest TDR, regardless of cultivation methods, but exhibited higher values in the monoculture pastures. Annual ryegrass tillers had the lowest TDR, independent of whether grown as monoculture or intercropped.

The black oat monocultures presented the lowest PSI throughout the growing season (mean value = 0.80), whereas the annual ryegrass pastures sown as monocultures or intercropped with the black oat presented higher values (average value = 0.92) (Table 1). Regarding months, PSI remained constant until September and then decreased in October.

Cohort survival diagrams

The cohorts that emerged after the second urea application contributed more than 80% of the TPD at the end of the experimental period, except for annual

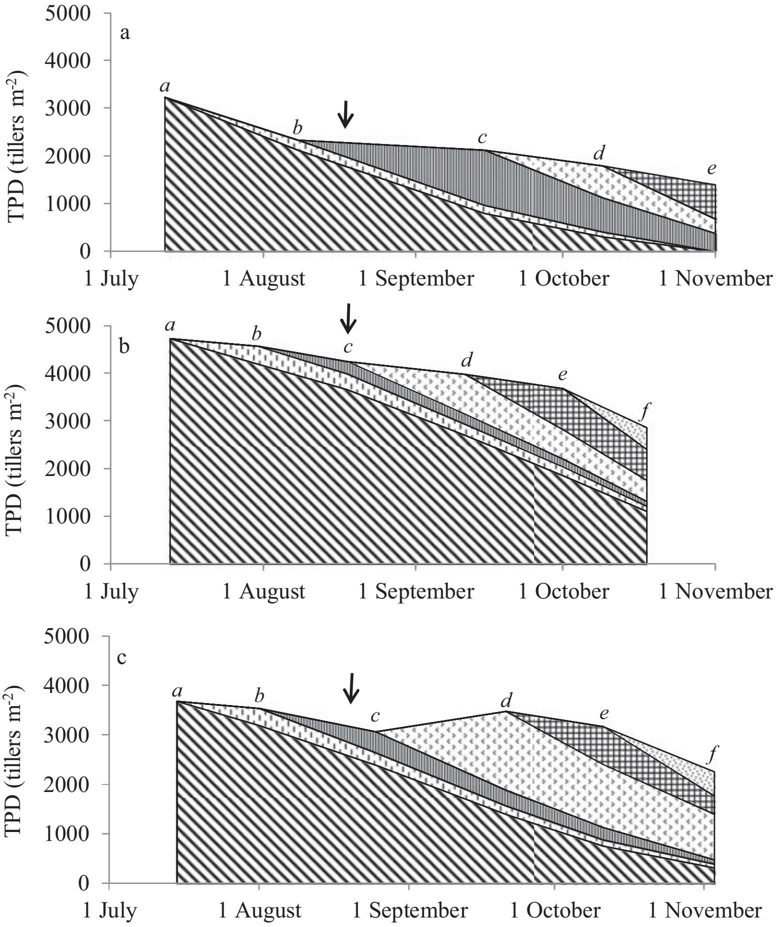

Figure 2. Cohort survival diagrams for black oat (*Avena strigosa* Schreb. 'IAPAR-61') and annual ryegrass (*Lolium multiflorum* Lam. 'Comum') tillers growing in monoculture (a and b, respectively) or intercropped (black oat + annual ryegrass tillers) (c). Arrows indicate the date when the second nitrogen fertilization was performed. Letters *a* to *f* represent the tiller cohorts.

ryegrass monocultures, which represented 59% of the final TPD, 37% being from the cohort *a* (Figures 2a, b and 3a, b). The black oat tillers that emerged prior to the second urea application did not survive (monoculture) or survived in small numbers (17% for intercropping) until the end of the experimental period (Figures 2a and 3a). The high TBR of annual ryegrass tillers during September in the intercropped pastures resulted in a positive change in TPD between the third and fourth evaluations (cohorts *c* and *d*) for this treatment (Figures 2c and 3b). From this point, annual ryegrass presented more tillers than black oat in the intercropped pastures, thus inverting the proportion that existed at the beginning of the experiment (Figure 3a and b).

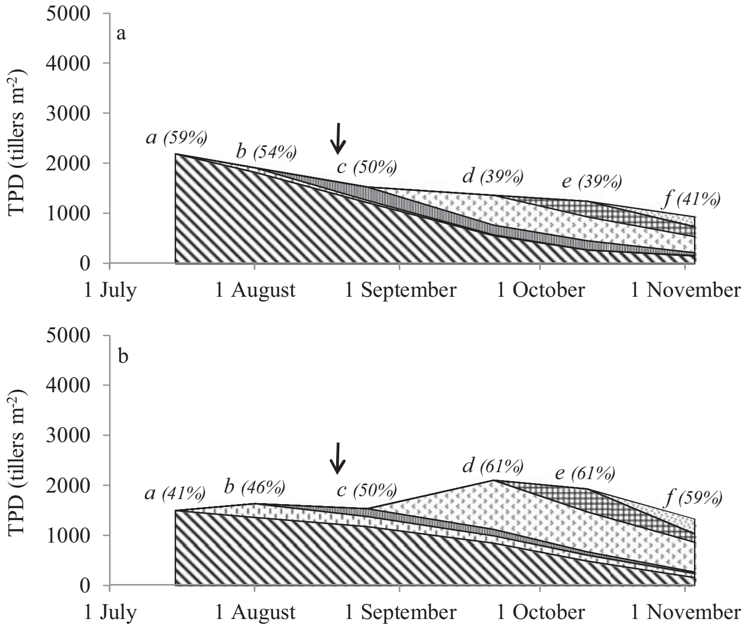

Figure 3. Cohort survival diagrams for tillers of black oat (*Avena strigosa* Schreb. 'IAPAR-61') (a) and annual ryegrass (*Lolium multiflorum* Lam. 'Comum') (b) intercropped. Arrows indicate the date when the second nitrogen fertilization was performed. Letters *a* to *f* represent the tiller cohorts and the numbers between parenthesis were the percent of the number of tillers of each species participating in the intercrop.

DISCUSSION

The three pastures evaluated presented distinct tillering patterns. Although monoculture presented constant reductions in TPD from the first to the last evaluated month, the high TDR values of black oat and low TBR of annual ryegrass directly influenced this pattern of response. In the intercropped pastures, the greater TDR of black oat associated with the elevated TBR of annual ryegrass, mainly in September, resulted in relatively constant TPD from July to September.

According to Bircham and Hodgson (1983), based on a study with a perennial mixture composed of *L. perenne*, *Poa annua* and *Trifolium repens*, there is a negative relationship between total population density (tillers + stolons) and forage mass. Possibly, in the present study, increments in pre-grazing forage mass until September (Duchini *et al.*, 2014) contributed to the increase in TDR during the first half of the pasture growing period through self-thinning mechanisms. Subsequently, the aging of the remaining tillers (especially of annual ryegrass) and the birth of small tillers (mainly in the black oat monoculture), which are highly susceptible to shading (Ong *et al.*, 1978), could be responsible for intensifying the TDR during the last half of the pasture growing season.

In intercropping, the lower TPD of black oat, compared to that of its monoculture, resulted in lower TDR for this species when intercropped, but it exhibited higher values than those found for annual ryegrass tillers. These results, together with the low rates of stem elongation found in black oat (Duchini *et al.*, 2016) and the low severity of applied defoliation (40% of the initial height), suggest that death of black oat tillers have a large genetic influence, generating low-longevity tillers (Figures 2a and 3a) with elevated mortality even when the forage mass was low (July and August). Regarding the annual ryegrass tillers, their TDR were systematically lower than those found in black oat, indicating that this species had a higher longevity, and thus demanded lower TBR to maintain pasture stability (Bahmani *et al.*, 2003; Matthew and Sackville-Hamilton, 2011).

The increase in TBR until September was primarily a consequence of an increase in TDR, which allowed a less dense canopy and likely a higher red:far-red irradiation reaching the plant bases (Casal *et al.*, 1985). This could partially explain the higher and lower average values for black oat and annual ryegrass in monocultures, respectively, and the intermediate values for intercropping (23.4 tiller 100 tiller^{-1}; considering both black oat and annual ryegrass tillers). However, TBRs were never high enough to exceed TDR in monoculture pastures, which may be related to the elevated seeding density associated with the relatively short growing season of these species. Moreover, the TBR reduction in October was caused by the transition from the vegetative developmental stage to the reproductive stage of both species (Duchini *et al.*, 2016).

The evaluation of TBR for both species in the intercropped pastures revealed an inversion in their tillering capacity when compared to their monocultures, with more elevated TBR for the annual ryegrass. This occurred because the opening of empty spaces between black oat plants, due to their elevated TDR, permitted the annual ryegrass to express its elevated tillering potential following the first grazing. From that point, the horizontal occupation by long-lived annual ryegrass tillers may have intensified the competition for light in the lower canopy strata, thus decreasing the TBR of black oat compared to their monoculture (Casal *et al.*, 1985). In this way, a tiller renovation and the alteration of the dominant species in September occurred, such that annual ryegrass accounted for approximately 60% of tillers present in the intercropped pasture (i.e. the inverse compared to July, when 41% of the tillers were from this species).

During the evaluation period, a nitrogen application was performed on August 22, causing increases in TBR during September with no decrease in TDR during the subsequent months. Caminha *et al.* (2010) studied the effects of N doses on marandu palisade grass and observed an increase in TBR without changes in TSR with applications of 150 kg of N ha^{-1}, when compared to pastures without fertilization. These results indicated that N input might be insufficient to maintain the stability of plants with elevated TDR, thereby necessary to include it with other strategy(s) to improve PSI. This is because high TBR may not be enough to compensate plants with very high TDR, once tiller bud site usage has a biological limit of approximately 0.69 (Neuteboom and Lantinga, 1989).

Because PSI is derived from the relationship between tiller survival and tiller birth, a diagram (Figure 4) was generated using both rates to facilitate discussion on the effect of each variable in the population stability of the studied pastures. In this way, it was evident that the highest observed PSI in July was a consequence of the lowest

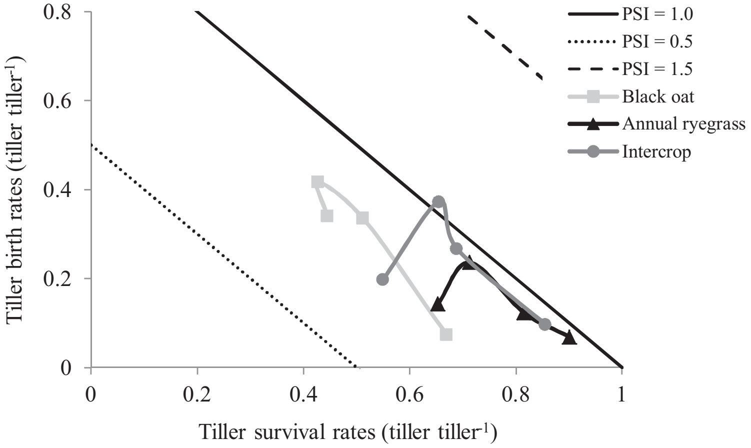

Figure 4. Population stability diagram of black oat (*Avena strigosa* Schreb. 'IAPAR-61'), annual ryegrass (*Lolium multiflorum* Lam. 'Comum') and intercropped (black oat + annual ryegrass) pastures over their monthly utilization. Data are represented with months in chronological order from the rightmost point, with each treatment represented separately.

TDR occurring during that month in all pastures because the lowest TBR were also found during that month. Similarly, the lowest PSI observed in October was caused by low survival rates associated with TBR declines because of the transition from the vegetative developmental stage to the reproductive stage. According to Bahmani *et al.* (2003), a decrease in tiller survival may indicate a decrease in pasture persistence, especially if stimuli for TBR increase do not occur once there will be a decrease in the number of buds able to generate new tillers (Chapman and Lemaire, 1993).

The low survival rates of tillers in pastures cultivated with black oat monocultures resulted in very low PSI throughout the growing season, indicating unstable pastures, which suggests the plants are more susceptible to the lack of growing factors even with an elevated TBR. These data indicate that this species can have a greater requirement for growing factors (water, light and nutrients) to maintain elevated herbage production levels. This may be one of the reasons that black oat monocultures presented the lowest gross growth rate during the vegetative stage and under the same conditions when compared to the others treatments (July–September: 69.1 kg DM ha^{-1} day^{-1} for black oat versus 88.8 kg DM ha^{-1} day^{-1} for annual ryegrass and intercropped pastures; Duchini *et al.*, 2016).

Regarding annual ryegrass and intercropped pastures, similar PSI was observed throughout the growing season. However, for each month, the PSI for intercrop shifted to the left when compared to annual ryegrass swards (Figure 4), indicating that the higher TSR for the annual ryegrass and the higher TBR for intercropped pastures (mainly coming from annual ryegrass) maintained the PSI of these treatments close to 1.0 during the first three months. It is important to highlight that, despite intercropped pastures exhibiting elevated PSI during that period, it is primordial to properly provide annual ryegrass tillering conditions during August and September

(South hemisphere), as the elevated TBR is directly related to response to N input and water.

CONCLUSION

Black oat and annual ryegrass present distinct tillering dynamics, whether in monocultures or intercropped with each other. The elevated tiller death rates for black oat in intercropping, and especially in monoculture, greatly increased the tiller birth importance for maintaining pasture stability. Conversely, the great longevity of annual ryegrass tillers indicates that annual ryegrass pastures are less sensitive to tiller birth rates for maintaining their stability. These results suggest that, in situations with risks of lack of resources (i.e. lower amount of fertilizers, risks of water shortage, and locations with very low temperatures and/or lighting), the utilization of black oat monoculture pastures would be more susceptible to loss of vigour and persistence when compared to pastures cultivated with annual ryegrass plants. However, these results also suggest that intercropping precocious species with elevated death rates (in this case, black oat) with later species (in this case, annual ryegrass), seems to be an important option for maintaining population stability throughout the growing season. Moreover, it should be reinforced that more studies are needed to advance the understanding of population dynamics of plants in multi-specific environments because various studies have pointed out that more diverse pastures have multiple benefits: they improve forage production and stability, enhance tolerance to climatic variations and mitigate possible environmental damage resulting from intensive animal production systems.

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DISCLOSURE STATEMENT

No potential conflict of interest was reported by the authors.

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