CHAPTER 2

Effect of clipping intensity on growth traits and competitive ability of forage grass

Based on: Jane Bemigisha, Sip E. van Wieren, Andrew, K. Skidmore, Alfred Stein, and Jan de Leeuw. (In review after revision, Grass and Forage Science). Initial growth and competitive ability of *Dactylis glomerata* and *Lolium multiflorum* in a clipping experiment

Abstract

The objective of this study was to establish how different intensities of defoliation affect growth characteristics and competitive ability of livestock forage grasses (*Lolium multiflorum* and *Dactylis glomerata)* at an early growth stage. A clipping experiment was set-up in a greenhouse at the Plant Sciences Experimental Center, Wageningen University and Research (WUR), in the Netherlands. The two species were grown in either mixed or monocultures and clipped three times at two five-week intervals. A nested Analysis of Variance (ANOVA) was used to test for effects of species type, species culture (monoculture or mixed), clipping height, and clipping time on plant height and dry matter (DM) yield of the two grasses. We found that clipping had greater effect on height than on dry matter yield, but increase in DM yield showed a stronger positive linear relationship with relative regrowth rate (RRR = 0.0008 + 0.0143* x ($p < 0.05$, $r^2 = 0.96$) than with height. Dry matter yield was also the dominant growth characteristic in monocultures for *D. glomerata,* and in mixed cultures for *L. multiflorum*. *L. multiflorum* showed a significantly higher relative regrowth rate than *D. glomerata* ($P < 0.05$), suggesting higher competitive ability. Our results conform to the notion that competition depends largely on growth rate. Further research may test this approach for understanding the effects of defoliation and species mix in forage grass species under livestock grazing and hay cutting considering various growth traits and environmental situations.

2.1 Introduction

Defoliation influences the growth and competitive interactions in forage plants (Grime, 1979). The effect of defoliation in the early established phase may significantly affect the competitive ability and survival of co-occurring forage species (e.g., Johnson *et al.,* 1983). The competitive ability of a plant may be studied based either on the competitive effect, implying the ability of an individual to suppress other individuals, or on the competitive response, implying the ability of an individual to avoid being suppressed, which relates to different abilities of plants to acquire and use resources (Goldberg, 1990). Tilman (1988) attributes the uncertainty surrounding predictions of competitive response and effect in the early stages of plant growth to the transient dynamics, which may be comparable to those in eventual vegetation patterns (e.g., Berendse *et al*., 1992). Research is therefore required on the short-term vegetation dynamics in the early established stages of plant growth (Goldberg, 1996; Tilman, 1988).

In interaction with defoliation, the uncertainty of the competitive response in forage plants may increase. For example, research on the combined effect of competition and grazing (e.g., Center *et al*., 2005; Flower and Rausher, 1985; Ilmarinen *et al*., 2005; Millett *et al*., 2005; Kuijper *et al*., 2004; Loo, 1993; Olff *et al*., 1999; Rodriguez and Brown, 1998; Vesk and Westoby, 2001) shows that these effects are not easily predicted because of the variable environmental context such as temperature, water, light and soil (e.g., Dayan *et al.,* 1981; Hardegree and Van Vactor, 1999; Höglind *et al*., 2001; Pronk, *et al*., 2007; Tilman, 1988; Riba, 1998), as well as various plant traits. Defoliation may change the ability of a plant to acquire limited resources such as soil nutrients and light by altering key morphological traits (Loud *et al*., 1990).

Grime (1979) identifies the characteristics determining the competitive ability of plant species in the early established phase to be storage organs, height, lateral spread, phenology, growth rate, response to stress, and response to damage. A more elaborate list of plant traits that have been correlated with competitive ability is provided in Goldberg (1996). Goldberg (1996) indicates that different studies show different predictions about traits correlated with competitive ability (Goldberg, 1996). Since the competitive traits differ among plant species, then the plant species' capacity to regrow following damage caused by defoliation may also differ.
The capacity to regrow may also be influenced by defoliation intensity. Studies on interactions of competition and defoliation have shown

that defoliation height is important (Loo, 1993). For example, following defoliation, re-initiation of the leaves of grasses at the base of the tiller forms subsequent leaf growth, depending on whether the leaf-forming meristems are low enough to escape damage (Langer, 1979). There is, therefore, need to identify traits that most correlate with competitive ability of specific plant species under different defoliation intensities.

Plant height is widely used in estimating competitive ability of plants because it is associated with the ability of a plant to compete successfully for light (Grime, 1979; Wallace and Verhoef, 2000). Height is particularly important during the initial growth stages because plants that become taller faster obtain a disproportionate share of the incident light, enhance their photosynthetic efficiency, and thus suppress the growth of other individuals (Tilman, 1988; de Wit, 1965). Pronk *et al.* (2007), however, suggest that plants may co-exist through different height growth strategies. This is related to the hypothesis that plant types with different heights can persistently co-exist over longer periods of time despite the competitive interactions (Pronk *et al.,* 2007). Therefore, a plant that grows taller may be considered a better competitor but this may not be consistent in all plant species and it is not easy to predict the persistence of this trait. This means that in spite of various investigations on plant height in response to defoliation and competition (e.g., Burboa-Cabrera *et al.,* 2003; Boyd and Svejcar, 2004; Navas and Moreau-Richard, 2005), research is still needed to estimate the extent to which plant height determines competitive ability.

Plant weight (biomass) and size are also widely used to determine competitive ability (Damgaard, 1999; Riba, 1998). Some studies show that larger plants have a higher absolute growth rate (Damgaard, 1999; Fetene, 2003; Riba, 1998). Competition however, seems to depend largely on growth rate, which is a product of dry weight (Tilman, 1988). Growth rate among species is expressed as relative growth rate and is commonly used to measure plant performance, including cases of defoliation (e.g., Damgaard, 1999; Humphrey and Schupp, 2004; Johnson *et al.,* 1983; Loo, 1993; Osem *et al.,* 2004). Relative growth rate is an increase in plant material per unit of material and per unit of time (Hunt, 1978). This means that a species that attains higher dry weight over a given time may be considered a better competitor. Since plant height may also determine competitive ability, this chapter focuses on both plant height and the weight (dry matter yield) of co-occurring forage grasses.

In a greenhouse experiment, we investigated the effects of species type, species culture, clipping height, and clipping time on the increase in height and dry matter yield of *Lolium multiflorum* and *Dactylis glomerata* in the early established phase of one growing season (vegetative stage). By comparing the increase in the height and dry matter yield with regrowth rate, we established the dominant competitive growth characteristic. The species that increased more in the dominant growth characteristic consistent with a high relative regrowth rate in mixed cultures was considered to have a higher competitive ability.

2.2 Materials and methods

2.2.1 Study species

The two forage grass species, *L. multiflorum* and *D. glomerata,* that were selected occur in Majella National Park, Italy, the study site related to this research (Chapter 5), where hay-cutting and grazing of livestock and wild animals combine. The two species are livestock forage grasses and widely used for hay. They have competitive growth characteristics. *L. multiflorum* (Annual ryegrass) is an annual or sometimes biennial bunch grass with a fibrous root system. It grows 30 to 100 cm tall. *L. multiflorum* is a highly palatable and digestible grass (Hannaway *et al.,* 1999). It is also known for its high yield potential, rapid establishment, and it is commonly used on heavy waterlogged soils (Hannaway *et al.*, 1999). On the other hand, Duke (1983) describes *D. glomerata* (Orchard grass or Cocksfoot grass) as a tufted fast-growing perennial, with a deep root system. It grows 20 to 120 cm tall. It grows rapidly, enabling it to out-compete most of the other plants. *D. glomerata* also thrives best on heavier types of soils such as clay and clay-loams, although it can also survive well in poor dry soils, and is drought-resistant. It is known to withstand heavy grazing (Cullen *et al.,* 2006), and gives a good aftermath if cut for hay (Duke, 1983). Under continuous heavy grazing, however, the persistence of *D. glomerata* declines significantly (Duke, 1983; Avery *et al*., 2000) and, if under-grazed, it becomes coarse and unpalatable (Duke, 1983).

2.2.2 Experiment set-up

2.2.2.1 Description of pot soils and seeding

D. glomerata and *L. multiflorum* seeds were sown on 14 December 2004 in a greenhouse at the Plant Sciences Experimental Center, Wageningen University and Research Center (WUR), in the Netherlands. Pots of 23 cm in diameter and 5 litres in volume were used. Potting soil was fertilized with 12.4%, phosphorous 14.2%, and potassium 13.8%. In each pot, we used a broadcast method to sow 40 seeds of either monoculture or a mixed culture. For the pots containing mixed cultures, 20 seeds of each species were sown.

2.2.2.2 Design of treatments and replicates

Altogether there were 18 replicates for each of the following twelve treatments: three combinations of species (monoculture of the two species and mixed culture) and four clipping heights (none, 5 cm, 10 cm, and 15 cm). The resulting 216 pots were placed according to a 6x6 design (Figure 2.1).

Clipping height levels were determined following Boyd and Svejcar (2004) and were maintained for all the clipping intervals. In this analysis, 10 cm and 15 cm are the clipping heights used for high and low clipping intensity, respectively, to simulate defoliation at low and high intensity.

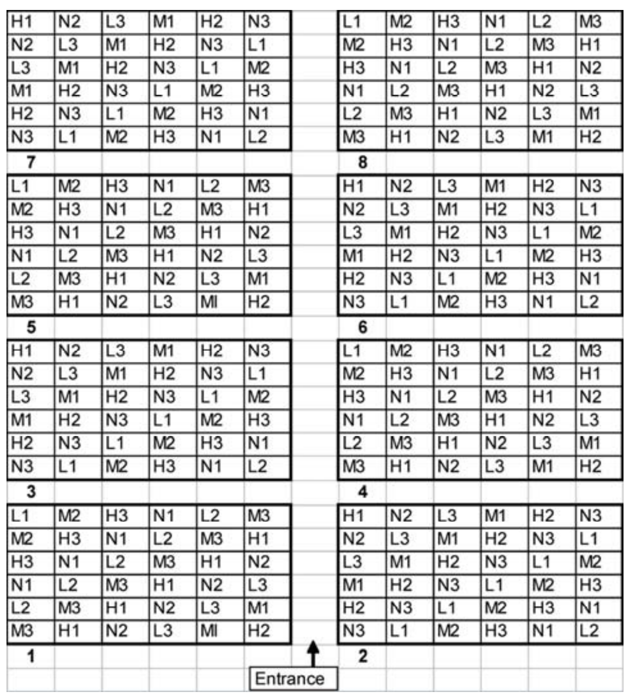

Figure 2.1 Set-up and treatment codes in the greenhouse. Clipping intensity treatments: L = Low, M = Medium, H = High, N = None; subjects (species): 1 = *L. multiflorum*, 2 = *D. glomerata*, 3 = mixed (*L. multiflorum and D. glomerata*).

2.2.2.3 *Growing conditions*

The grasses were planted in a greenhouse with environmental conditions imitating the summer growing season of Majella National Park, Italy: day temperature 20°C and night temperature 15°C; natural daylight and additional light from 400 W AGRO-SON-T Phillips lamps to provide 16 hours of light; outdoor humidity; normal air; and adequate watering. The greenhouse conditions were set at the same level to ideally demonstrate competitive ability given the same natural habitat as may be for naturally co-occurring species following a strategy used in the Zone of Influence (ZOI) model (Gates, 1980). In the ZOI model equivalent resources are distributed uniformly over an area in the analysis of competition (Gates, 1980).

2.2.3 Clipping treatments and measurements

Clipping was done at five-week intervals, starting on 3 February 2005. The intervals were at T1: eight weeks, T2: 13 weeks and T3:18 weeks after sowing following Hannaway *et al.* (1999), and a later review (Cullen *et al*., 2006). Before clipping, the average height of grass plants in each pot was obtained from measurement with a metric ruler against leaves in a pulled upright form. In the mixed cultures, separate height measurements were taken for each species. The clipped plant material was dried at 70°C for three hours and at 105°C for another 10 hours. As in height measurement, the weight of the dried matter was measured per unit (pot), maintaining separate weight for each species in the mixed cultures. Prior to analysis, the dry weight of monocultures (sown with 40 seeds) was divided by two to enable comparison with mixed cultures (20 seeds of each of the two species). Table 2.1 presents the data on height (cm) and dry matter (g).

2.2.4 Analysis

Using a nested analysis of variance (ANOVA) in STATISTICA by StaSoft Inc., USA, we investigated the effect of species type (*Dactylis* and *Lolium*), species culture (monoculture and mixed), clipping height and time of clipping on the increase in height and dry matter yield of *L. multiflorum* and *D. glomerata.* In a nested analysis, levels of one factor occur in combination with the levels of one or more other factors, and different levels occur in combination with others at the next level (Zar, 1996). For this study, the species have different levels of cultures, and the cultures have different levels of clipping height, while clipping was at three different times (T1, T2 and T3). Figure 2.2 illustrates the nested model used in this study. Only variables of T2 and T3 were used in the analysis because T1 was the base clipping time. Table 2.1 shows the mean height (cm) and dry matter (g) according to the analysed factor levels. Rather than the functional or dynamic approach (e.g., de Wit *et al.*, 1978; Tilman, 1988), a simpler approach was used by calculating growth parameters (dry matter yield (g) and height (cm) across one harvest interval as done in Hunt *et al.* (2002).

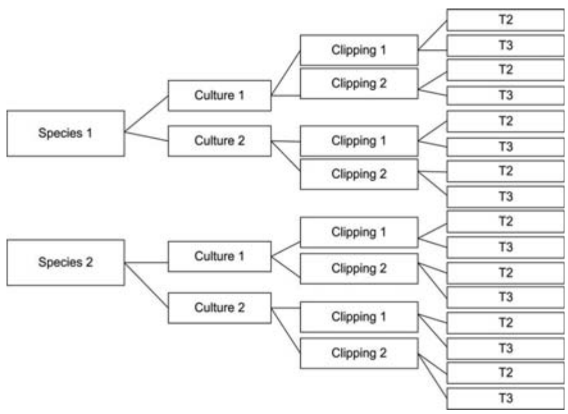

Figure 2.2 An illustration of the nested ANOVA model used. Clipping time nested in clipping height nested in culture and species. Species 1 and 2 are *D. glomerata* and *L. multiflorum*; Culture 1 and 2 are monoculture and mixed culture respectively; Clipping 1 and 2 indicate Low (15 cm) and High (10 cm); T2 and T3 indicate clipping at 13 weeks and 18 weeks after sowing, respectively.

The following model indicates that the effect of clipping time is nested within the interaction effects of species × culture × clipping height.

G = (Species*Culture* Clipping)/Time

The following terms are used to express the model:

G_{ijknl} = ($Species_i$*$Culture_j$*$Clipping_k$) $Time_n$ + e_{ijknl} (Eq.2.1) where:

G_{ijkl} = the mean growth response variable, i.e., height or dry weight

$Species_i$ = *D. glomerata* (for i = 1) and *L. multiflorum* (for i = 2)

$Culture_j$ = monoculture (for j = 1) and mixed culture (for j = 2)

$Clipping_k$ = clipping height, i.e., low clipping at 15 cm height (for k = 1) and medium clipping at 10 cm height (for k =2)

$Time_n$ = T2 and T3, i.e., clipping time interval 2 (13 weeks after sowing) (for n = 1) and clipping time interval 3 (18 weeks after sowing) (for n = 2)

e_{ijknl} = a normally distributed error term with mean zero.

The effect was considered significant at $P \leq 0.05$, and if $F_{Observed} > F_{Expected}$. A Scheffé *post hoc* test using $P = 0.05$ significance level was used to establish the specific pairs of treatments that significantly differed from each other.

We established the competitive ability by using relative regrowth rate (RRR) based on the relative growth rate formula (Hoffman and Hendrik, 2002):

$$RRR = \frac{\overline{\ln(W_3} - \overline{\ln(W_2})}{t_3 - t_2} \qquad \text{(Eq.2.2)}$$

where $\overline{\ln(W_2})$ and $\overline{\ln(W_3}$) are the mean of the natural log of dry weight at two clipping dates, t_2 and t_3. The RRR is the difference in the mean of the natural log of dry weight at the two clipping intervals. Our definition includes only the growth increment minus remaining stubble at the previous time of clipping (dry matter (g) of re-sprouted plant tissue clipped or removed between clipping intervals)), which differs from relative growth rate. Height regrowth was defined as the difference between the average plant height at clipping T2 and T3.

To establish the species that showed higher competitive ability and the growth characteristic that was more consistent with relative regrowth rate, a paired *t*-test was used to test for differences between regrowth in height versus regrowth in dry matter yield, regrowth in height versus relative regrowth rate, and regrowth in dry matter yield versus relative regrowth rate. Scatter plots were used to show the relations.

Table 2.1 Mean height (cm) and mean dry matter (DM g) with 95% confidence intervals for species, *D. glomerata* and *L. multiflorum* in monocultures and mixed cultures under low intensity (15 cm height) and high intensity clipping (10 cm height), clipped at T2: 13 weeks after sowing and T3: 18 weeks after sowing.

T2: 13 weeks after sowing

Species	*Culture*	*Clipping height (cm)*	*Average height (cm) (n = 18)*			*DM (g) (n = 18)*		
			Ht (cm)	-95%	+95%	DM (g)	-95%	+95%
D. glomerata	Mixed	15	29.41	27.63	31.20	9.09	8.41	9.77
		10	28.50	26.76	30.22	8.67	7.99	9.36
	Mono-	15	37.56	35.77	39.34	6.66	5.98	7.34
	culture	10	36.58	34.85	38.32	7.11	6.64	8.00
	Mixed	15	32.03	30.25	33.81	12.2	11.49	12.85
L. multiflorum		10	30.33	28.60	32.06	11.5	10.86	12.22
	Mono-	15	32.03	30.25	33.81	6.21	5.53	6.89
	culture	10	29.25	27.52	30.98	7.37	6.68	8.05

T3: 18 weeks after sowing

Species	*Culture*	*Clipping height (cm)*	*Average height (cm) (n = 18)*			*DM (g) (n = 18)*		
			Ht (cm)	-95%	+95 %	DM (g)	-95%	+95%
D. glomerata	Mixed	15	32.29	30.64	33.95	9.16	8.61	9.70
		10	31.18	29.50	32.83	8.76	8.23	9.29
	Mono-	15	37.72	29.11	32.33	7.91	7.36	8.45
	culture	10	36.33	34.72	37.94	8.51	7.98	9.04
L. multiflorum	Mixed	15	33.12	31.44	37.76	13.45	12.91	14.00
		10	31.82	30.17	33.48	13.62	13.09	14.15
	Mono-	15	30.72	29.11	32.33	6.98	6.46	7.51
	culture	10	31.00	29.39	32.61	7.54	7.01	8.07

2.3 Results

2.3.1 Effect of clipping and species on height

We tested for the effects of clipping time, clipping height, species cultures and species on height and found that the effects were highly significant (Table 2.2). The results from the nested ANOVA showed that height was significantly affected by species (F12, 264 = 31.56; $P < 0.001$), culture ($F_{12, 264} = 43.05$; $P < 0.001$), clipping ($F_{12, 264} = 8.3$; $P < 0.005$), and time nested within these interactions ($F_{12, 264} = 8.23$;

$P < 0.001$). Figure 2.3 shows the mean height (cm) for *D. glomerata* and *L. multiflorum* in mixed cultures and monocultures and clipping intensity at 15 cm height and 10 cm height above the ground. The letters on top of the bars show significance of the differences between pairs according to the Scheffé *post hoc* test. Comparing the increase in height of the two species, the mixed cultures of *D. glomerata* under both low (15 cm) and high (10 cm) clipping heights was lower than that of *L. multiflorum*, but in the monocultures the reverse was true. Between T2 and T3, the mean height in both mixed cultures and monocultures of *D. glomerata* clipped at low clipping height increased significantly ($P < 0.05$), but this was not the case with the higher clipping height.

On the other hand, the *L. multiflorum* monoculture under low clipping showed a decrease in height, whereas under high clipping an increase was shown. Table 2.1 shows the mean height with 95% confidence intervals. *L. multiflorum* showed 4% higher average height than *D. glomerata* in mixed cultures at T2 and the difference was significant ($P < 0.05$), but the difference at T3 was only 2%. In the monocultures, height in *D. glomerata* was 12% higher than that of *L. multiflorum* and the difference was significant ($P < 0.05$). The difference at T3 was significant ($P < 0.05$).

In summary, the height of *D. glomerata* in the mixed cultures and at both low and high clipping heights was lower than that of *L. multiflorum,* but in the monocultures the reverse was the case. The potential of *D. glomerata* to grow taller was not realized in the mixed culture. Between the T2 and T3 clipping interval, the difference in height between the two species decreased.

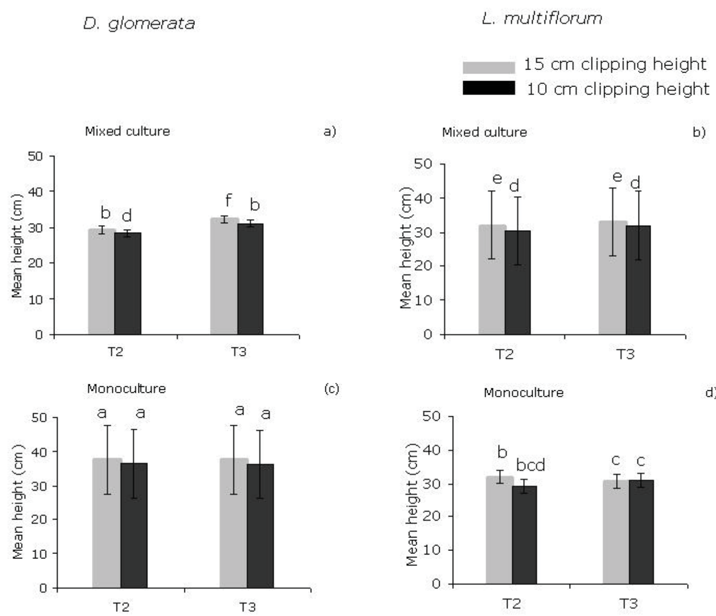

Figure 2.3 Mean height (cm) of *D. glomerata* and *L. multiflorum* in mixed cultures (a and b) and monocultures (c and d) clipped at low (15 cm height above the ground) and high clipping intensity (10 cm height) at T2:13 weeks after sowing and T3:18 weeks after sowing. Pairs that are labelled with different letters were found significantly different by the Scheffé *post hoc* test ($P \leq 0.05$). Vertical bars (whiskers) denote 0.95 confidence intervals

Table 2.2 Nested ANOVA results: effect on height of clipping time nested in clipping, culture and species

Effect	SS	DF	MS	$F_{\_ Observed}$	*P*
Species	406	1	406	31.56	< 0.001
Culture	554	1	553.9	43.05	< 0.001
Clipping	107	1	106.8	8.3	< 0.01
Time (Species*Culture*Clipping)	1271	12	105.9	8.23	< 0..001
$F_{\_Expected}$: $F_{12, 264}$=8.2334, P < 0.001					

2.3.2 Effect of clipping and species on dry matter

Results from the nested ANOVA (Table 2.3) show significant differences in dry matter owing to the effects of the two species ($F_{12, 305}$ = 122.1; $P < 0.001$), culture ($F_{12, 305}$ = 581.7; $P < 0.001$), clipping height ($F_{12, 305}$ = 24.1; $P < 0.001$), and time of clipping nested within these interactions ($F_{12, 305}$ = 24.1; $P < 0.001$). Clipping height alone had no significant effect. Figure 2.4 shows the mean dry matter (g) for *D. glomerata* and *L. multiflorum* in mixed cultures and monocultures and clipping intensity at 15 cm height and 10 cm height above the ground. The letters on top of the bars indicate significance in the differences between treatment pairs according to the Scheffé *post hoc* test. The dry matter of *D. glomerata* monocultures clipped at low clipping height (15 cm) was higher in the mixed than in the monocultures and the difference was significant ($P < 0.05$). Unlike in the mixed cultures, the dry matter yield in monocultures of *D. glomerata* increased significantly ($P < 0.05$) between T2 and T3. On the other hand, at T2, when *L. multiflorum* was clipped at low rather than high clipping height, the dry matter yield was higher. The dry matter yield of *L. multiflorum* in mixed cultures increased significantly at T3, particularly at 10 cm (high clipping intensity) ($P < 0.05$). This was significantly higher than for *D. glomerata* ($P < 0.05$) at the same 10 cm clipping height, where the dry matter yield increased by only 0.09 g (Table 2.1).

Therefore, in both species dry matter yield in the mixed cultures was lower under low clipping intensity (15 cm) than under high clipping intensity (10 cm) but the reverse was true for monocultures. In monocultures, the dry matter yield of *D. glomerata* was higher but in mixed cultures it was lower than height.

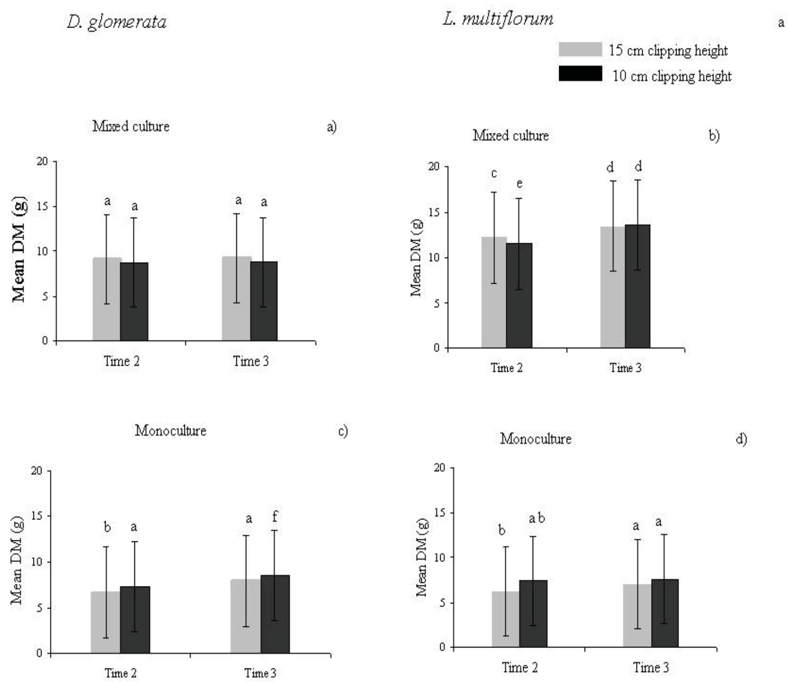

Figure 2.4 Mean DM of *D. glomerata* and *L. multiflorum* in mixed cultures (a and b) and monocultures (c and d) under low clipping intensity (15 cm clipping height above the ground) and high (10 cm clipping height), at T2:13 weeks after sowing and T3:18 weeks after sowing. Pairs that are labelled with different letters on top of the bars were found significantly different according to the Scheffé *post hoc* test ($P \leq 0.05$).Vertical bars (whiskers) denote 0.95 confidence intervals.

Table 2.3 Nested ANOVA results: effect of time nested in clipping, culture and species on dry matter

Effect	*SS*	*DF*	*MS*	*F_ Observed*	*P*
Species	194.5	1	194.5	122.1	< 0.001
Culture	926.8	1	926.8	581.7	< 0.001
Clipping	3.5	1	3.5	2.2	> 0.1
Time(Species*Culture*Clipping)	460	12	38.3	24.1	< 0.001
$F\_{expected}$: $F_{12, 305}$=24.058, p < 0.001					

2.3.3 Height and dry matter yield vs. relative regrowth rate

L. multiflorum increased more in dry matter yield and regrowth rate than did *D. glomerata*. (Table 2.4, Figure 2.5). Table 2.4 shows an increase in regrowth of the height and dry matter yield of *D. glomerata* and *L. multiflorum* and their relative regrowth rate. The Table 2.1 data were used to compute the regrowth and relative regrowth rate. In monocultures the height of *D. glomerata* clipped at low (15 cm) height increased, whereas that of *L. multiflorum* decreased. Dry matter yield increased in *D. glomerata* by 1.25 g. This was higher than the increase of 0.78 g in *L. multiflorum*. The higher increase in height and dry matter yield of *D. glomerata* was consistent with the higher relative regrowth rate of 0.017 gw^{-1} (RRR of *L. multiflorum*: 0.012 gw^{-1}). In the monocultures clipped at high intensity (10 cm height), however, the height of *D. glomerata* decreased by 0.25 cm, whereas that of *L. multiflorum* increased by 1.75 cm. The increase in dry matter yield of *D. glomerata* (1.19 g) was higher than that of *L. multiflorum* (0.17), and this was consistent with the relative regrowth rate, which was higher for *D. glomerata* (0.015 gw^{-1}) than for *L. multiflorum* (0.007 gw^{-1}).

In mixed cultures, *D. glomerata* clipped at low clipping height increased in height by 2.88 cm, whereas *L. multiflorum* increased by only 1.09 cm. As regards dry matter yield, the positions were reversed, with *D. glomerata* increasing by only 0.07 g and *L. multiflorum* increasing by 1.28 g. *L. multiflorum* showed a higher relative regrowth rate (0.020 gw^{-1}) than *D. glomerata* (0.001 gw^{-1}). In mixed cultures under higher clipping height, *D. glomerata* increased in height by 2.68 cm, which was almost twice that achieved by *L. multiflorum* (1.49 cm). Under low clipping height, the reverse was true as regards dry matter yield. The dry matter yield of *L. multiflorum* (2.12 g) increased more than that of *D. glomerata* (0.09 g). The relative regrowth rate for *L. multiflorum* (0.003 gw^{-1}) was higher than that for *D. glomerata* (0.001 gw^{-1}). The results of the *t*-test (tabulation not shown) showed that the regrowth of *L. multiflorum* was significantly higher than that of *D. glomerata* ($P < 0.05$).

Clipping had greater effect on height than on dry matter yield but the increase in dry matter yield was more consistent with relative regrowth rate. Figure 2.5 shows a strong positive linear relationship for relative regrowth rate versus regrowth in dry matter (RRR = 0.0008 + 0.0143* x ($p < 0.05$, $r^2 = 0.96$). The increase in relative regrowth rate with dry matter yield was not evident in height. *L. multiflorum* was therefore considered to have higher competitive ability because it showed a higher increase in the dry matter yield of the mixed cultures and a more positive relationship with relative regrowth rate.

Table 2.4 Mean regrowth in height (cm), DM (g), and relative regrowth rate (g week^{-1}) of *D. glomerata* (Dt) and *L. multiflorum* (L) in monocultures and mixed cultures under low and high clipping intensities. The mean height and DM regrowth are obtained from Table 2.1, section 2.2.4.

Species	Culture	Clipping Height (cm)	Mean height regrowth (cm)	Mean DM regrowth (g)	RRR (g week^{-1})
Dt	Mono	15	1.16	1.25	0.017
Dt	Mono	10	- 0.25	1.19	0.015
Dt	Mix	15	2.88	0.07	0.001
Dt	Mix	10	2.68	0.09	0.001
L	Mono	15	- 1.31	0.78	0.012
L	Mono	10	1.75	0.77	0.007
L	Mix	15	1.09	1.28	0.020
L	Mix	10	1.49	2.12	0.033

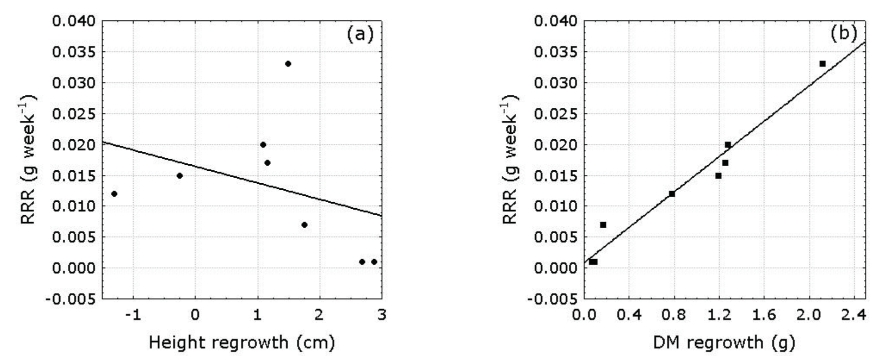

Figure 2.5 Relationship between (a) regrowth in height (cm) with RRR (g week^{-1}) and (b) regrowth in DM with RRR (g week^{-1}). A strong positive linear relationship is shown for RRR versus regrowth in DM: RRR = 0.0008 + 0.0143* x ($p < 0.05$, $r^2 = 0.96$).

2.4 Discussion

A strong positive linear relationship between relative regrowth rate and regrowth in dry matter was shown, but not with height (Figure 2.5). These results are comparable to those in the studies carried out by Navas and Moreau-Richard (2005), who found no relationship between species competitive response and height. The results are also comparable to the findings by Burboa-Cabrera *et al*. (2003) on grazing intensity and tiller height. Although the potential of *D. glomerata* to grow taller was not realized in the mixed cultures, the increase in dry matter yield enabled a higher competitive ability, whereas *L. multiflorum,* which is believed to grow larger and germinated two weeks earlier, did not show this trait in monocultures.

The advantage of early germination and establishment in *L. multiflorum* was in agreement with Humphrey and Schupp (2004) and with Kuijper *et al*. (2004) that early emergents usually become taller and more competitive (Tilman, 1988). This notion would not hold entirely for this study, since, rather than the increase in grass height, increase in dry matter yield was the dominant trait. As seen before, plant weight and size have also been related to competitive ability (Damgaard, 1999; Fetene, 2003; Riba, 1998; etc.). The results confirm this and suggest that the early establishment, larger stature and higher dry matter yield of *L. multiflorum* contributed to its higher relative regrowth rate and higher competitive ability in the mixed cultures. This is in conformity with the notion that competition depends largely on growth rate, which is a product of dry weight (Tilman, 1988).

The link between the response to competition and plant size is not, however, universal (Navas and Moreau-Richard, 2005) and has not, to the knowledge of the authors, been investigated in monocultures. In this study, the increase in dry matter yield was not significantly affected by clipping unless in interaction with culture and species. The results suggest that, more than grazing intensity, culture and species may influence the competitive ability of *D. glomerata* and *L. multiflorum*.

The greater significance of dry matter yield over plant height in the competitive interactions was found for *L. multiflorum* in mixed cultures. In mixed cultures clipped at low intensity (15 cm), positions were reversed for the species. *L. multiflorum* showed higher regrowth under both low and high clipping intensities (Table 2.4). Furthermore, the results of the *t*-test showed that the regrowth of *L. multiflorum* was significantly higher than that of *D. glomerata* ($P < 0.05$). The higher dry matter yield and relative regrowth rate *of L. multiflorum* in mixed cultures suggests that it has a higher competitive ability.

D. glomerata was found to have higher dry matter yield in the monocultures. The findings suggest that *D. glomerata* has the potential to out-compete *L. multiflorum*. Moreover, *L. multiflorum*, being an annual species already showed signs of senescence by the end of the experiment while *D. glomerata* was still growing. This suggests that the dominance of the former species may be reversible later in the growing season. However, the scope of this research did not cover such an investigation.

It has been shown that, in the absence of *L. multiflorum, D. glomerata* becomes more productive over time, whereas the contrary is true when the two are mixed. In the mixed cultures, *L. multiflorum* showed higher dry matter yield and relative regrowth rate and therefore a higher positive response to inter-specific competition than to intra-specific competition. The results suggest that defoliation pressure on *L. multiflorum* is more detrimental if the species is occurring in monocultures than if it is co-occurring with *D. glomerata*.

Both species showed higher regrowth in mixed cultures than in monocultures. This may be because the species have a positive effect on each other, with *L. multiflorum* showing higher competitive ability. Rodriguez and Brown (1998) found comparable results in *P. annua,* which showed significantly greater biomass in mixed stands than in monocultures. Similar results are reported by Flower and Rausher (1985). In their study on the performance of single versus mixed plant species, Kuijper *et al.* (2004) found that at the lowest nitrogen level the performance of two species decreased when grown together rather than in monocultures.

Regrowth was higher under high clipping intensity (10 cm) than under low intensity (15 cm). Relative regrowth rate was also higher in the mixed cultures clipped at high intensity than in those clipped at lower intensity (Table 2.4, Figure 2.4). This shows a positive effect of higher defoliation intensity on the growth of the two species. Other studies have found that some plants benefit from defoliation damage by grazing through overcompensation (e.g., Riba, 1998), although other studies (e.g., Lucas *et al.,* 2004) have not found this effect. In another study, longer lax grazing has led to increased tiller density and herbage production (Garay *et al.,* 1997). Grasses are well adapted to being grazed or cut if, before the flowering stage is reached, leaf formation continues during and after subsequent defoliation (Langer, 1979). During the vegetative phase, the meristematic zones are usually located close to the soil surface beyond the reach of animals and cutting machines. Even if some meristems are removed by defoliation, they may readily be replaced by the appearance of new tillers (Langer, 1979). The duration of this experiment was limited to the vegetative stage of growth in both species. This may be a reason why higher clipping did not have the expected higher detrimental effect.

Therefore, the two species seem to attain higher productivity when mixed and clipped at higher intensity (10 cm above the ground) than when growing separately and clipped at lower intensity (15 cm). Further research should investigate clipping height and species mix for guiding stocking density and hay cutting at field level.

Relative regrowth rate could also have been affected by the traits and other factors not investigated in this study. There are numerous traits that may be considered including emergency and establishment, tiller and leaf appearance rate, leaf area expansion rate, plant longevity, defence investment (Goldebrg, 1996; Navas and Moreau-Richard, 2005; Kuijper *et al*., 2004; Damgaard, 1999; Espigares *et al*., 2004). Although such traits affect shoot regrowth, equally important are the environmental factors (Dayan *et al.,* 1981; Vesk and Westoby, 2001).

Some factors have direct interaction with the traits, for example, light interception (de Wit, 1965; Johnson et *al.,* 1983; Tilman 1988), substrate size and nitrogen use efficiency (Loo, 1993), and temperature (e.g., de Wit, 1978; Hardegree and Van Vector 1999; Loo, 1993). Dayan *et al*. (1981) argue that an accurate prediction of the growth of grasses under defoliation should include the number, size, and phenological state of the tillers present at the moment of cutting, the current level of carbohydrate reserves, and the residual green leaf area. Loo (1993) includes cutting frequency, while others (e.g., Garay *et al.,* 1997; Hitchmough *et al*., 2004) add seeding rate, timing and duration of grazing. However, insight is gained by taking a simple perspective and exploring the implications of a few factors, with other potentially important factors "held constant" for the sake of ease of analysis (Tilman, 1988).

In this study, we demonstrate that traits which determine competitive ability in the early established stage of the studied forage grass species can be identified through a short-term experiment. Such experiments reasonably explore vegetation growth processes that would require long-term empirical studies (e.g., Johnson *et al.,* 1983). This means that competitive ability of the various co-occurring forage species in the early established stage of growth may be more efficiently established. Whether the species that have initial relatively higher yields eventually replace the other species, however requires further research.

2.5 Conclusions

This research has established that clipping has a more significant effect on height than on dry matter yield, and that increase in dry matter yield determines the relative regrowth rate in the species. Our results are in conformity with the notion that competition depends largely on growth rate.

A dominant growth characteristic (dry matter yield) can be identified during the early establishment stages of *D. glomerata* and *L. multiflorum* when the two are grown in monocultures and mixed cultures under variable grazing intensity. *L. multiflorum* attained higher dry matter yield, consistent with higher regrowth and regrowth rate and therefore higher competitive ability. Therefore, traits that determine competitive ability can be identified in such a short-term experiment. Further investigation is needed to establish if the dominance of the trait to increase in dry matter yield and the competitive ability of *L. multiflorum* may be sustained beyond the current experiment time.

The two species may be more productive when mixed and clipped at high intensity (10 cm above the ground) than when growing separately and clipped at lower intensity. This needs to be investigated further considering optimal clipping height and species mix for guiding stocking density and hay cutting at field level.

At field level, selective grazing may reduce the competitive ability of preferred forage species if the suppression of their regrowth by higher grazing intensity is greater than that in co-occurring less preferred ones. This leads to vulnerability of preferred forage species. Using the same experiment set up, the regrowth capacity of the two species under selective clipping is, therefore, investigated in the next chapter.