

CHAPTER 3

CULTIVAR EFFECTS OF PERENNIAL RYEGRASS ON HERBAGE INTAKE BY GRAZING DAIRY COWS

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Abstract. Perennial ryegrass is the most abundant grass species in temperate climates. An increased herbage intake of dairy cows by breeding new cultivars could have a large potential impact on agriculture. The effects of cultivars on sward structure, nutritive value, physical characteristics and disease resistance of perennial ryegrass are discussed. Cultivar differences were found in several studies for plant factors such as dry-matter yield, green-leaf mass and bulk density. Clear cultivar differences in nutritive value of perennial ryegrass were observed, especially the cultivar rankings for concentrations of water-soluble carbohydrates and acid detergent lignin were found to be consistent during the season and across years. Cultivar effects were also found for physical characteristics, e.g., tensile strength and resistance against crown rust (*Puccinia coronata* f. sp. *lolii*). The different plant-related cultivar effects were evaluated for their effects on herbage intake by grazing dairy cows. Differences among cultivars for the concentration of water-soluble carbohydrates affected the preference behaviour of dairy cattle. The possibilities to enhance dry-matter intake in a grazing situation through breeding can mainly be achieved by selecting for a better crown-rust resistance and a higher dry-matter production. A higher dry-matter production would give more opportunities for selection by dairy cows and might, therefore, enhance herbage intake at the animal level, but the production of more herbage would certainly enhance herbage intake at farm level.

Keywords: plant factors; herbage intake; preference; grazing

INTRODUCTION

Perennial ryegrass is the most abundant species in pastures of temperate climate zones such as Northwest Europe or New Zealand, and is generally considered a high-quality fodder (Bonthuis et al. 2004). An agronomically good sward should botanically consist of over 50 % perennial ryegrass (De Vries et al. 1942; Neuteboom 1986). The annual genetic improvement for dry-matter (DM) yield of perennial ryegrass was estimated to be proportionally 0.5 % in the period from 1965 to 1990 (Van Wijk and Reheul 1991). This gain was mainly due to increased persistence of the new varieties, resulting in an increase in DM yields in the third and fourth year after establishment (Van Wijk et al. 1993). Yield potential is an important characteristic in the Dutch Recommend List of Varieties.

A farmer benefits from this improved yield by producing more forage on the farm or by producing the same amount of forage at lower fertilizer rates. In this way, new cultivars contribute to a better use of nutrients (Visscher 1998). Grass is mainly used as feed in animal-production systems and for dairy production in particular. One can question whether farmers benefit most from testing programmes that are focused on grass yield parameters only. Farmers benefit most from an efficient conversion of herbage into milk. However, until now little attention has been given to characteristics that can promote herbage intake of grazed perennial ryegrass (Gilliland et al. 2002), a factor that still limits the milk production and maintenance of live-weight of highly productive dairy cows (Chilibroste 1999; Taweel 2004). The official Dutch testing programmes do not include quality parameters, such as *in vitro* digestibility, or chemical composition for perennial ryegrasses. In contrast, forage maize (*Zea mays* L.) cultivars are tested for specific quality traits in The Netherlands, e.g. *in vitro* digestibility (from 1983 onwards), starch content (from 1999 onwards) and cell-wall digestibility (from 2002 onwards). Testing programmes for perennial ryegrass in the UK or Australia include *in vitro* digestibility, or high sugar content (Gilliland et al. 2002; Smith et al. 2001).

PLANT FACTORS

Sward structure and morphology

Sward structure is an important quality aspect of grass with respect to intake and digestibility (Laca et al. 1992; Laidlaw and Reed 1993). Sward structure includes herbage mass, sward surface height, bulk density and tiller density, and morphological and botanical composition. While measurement of sward characteristics is vital for the understanding of animal-sward interactions, the techniques to measure them are time-consuming and labour-intensive. Notwithstanding that, it is essential to give a full description of the sward to allow full interpretation of the intake data (Laidlaw and Reed 1993). Differences in sward structural characteristics among grass species are well recognized, but more recently such differences have also been found among perennial-ryegrass varieties, as shown in Table 1.

Herbage mass

Cultivars of perennial ryegrass have different yielding capacities; this is well-known and yield potential is a main breeding target. The average annual yield might differ among cultivars about 10-15 % (Table 1), but large differences are generally found among the various cuts within a season, and across years. The start of the growing season will be earlier when using early heading cultivars; however, the annual yield might be higher using late heading cultivars (Gilliland et al. 2002; Gowen et al. 2003). Ploidy showed to have an effect on herbage mass. Nevertheless, authors are not consistent in their findings. Gilliland et al. (2002) found in a one-year cutting trial that tetraploids had higher values for biomass, extended tiller height and bulk density. O'Donovan (2001) found opposite results in a two-year grazing trial, where tetraploids had lower values for biomass and bulk density. Orr et al. (2001) tested 9

diploid and 6 tetraploid cultivars under both simulated grazing (8 cuts per year) and continuous stocking with sheep. They found that tetraploid cultivars had a higher biomass under cutting, but there were no differences between ploidy levels under grazing.

Herbage mass can have a significant effect on the herbage intake of the individual animal (Meijs 1981). Herbage mass can have both positive and negative effects on herbage intake. In a stall-feeding situation, high-yielding cultivars were consumed less (Figure 1A) (Tas et al. 2005), but a grazing situation, the high-yielding cultivars were consumed more (Figure 1B) (Smit et al. 2005b). In a stall-feeding situation, dairy cows can consume a homogeneously cut herbage that is available *ad libitum*, and the quality of the sward is the most important factor (Minson 1987). Quality, e.g., digestibility, decreases with a higher dry-matter yield (DMY) per cut; therefore the consumption of herbage harvested at a high herbage yield will decrease (Beever et al. 2000).

Table 1. Overview of variation in sward structural characteristics found in perennial-ryegrass cultivars as presented in the literature

Reference	Number of cvs.	Cutting height	Exp. year	Mean	Max.	Min.	Cultivar effects
Dry-matter yield cut¹ (tons ha⁻¹)							
Orr et al. (2001)	15		1998	1.71	2.03	1.54	***
			1999	1.33	1.51	1.23	***
Gilliland et al. (2002)	12	3 cm	2000	1.30	1.42	1.13	***
Gowen et al. (2003)	4	4 cm	1999	2.18	2.41	1.96	***
			2000	2.45	2.62	2.29	***
Smit et al. (2005a)	6	6 cm	2000	2.21	2.29	2.07	**
			2001	2.36	2.76	2.24	***
Smit et al. (2005b)	4	4 cm	2002	2.09	2.20	1.93	***
	4		2003	2.25	2.43	2.10	**
Sward surface height (cm)							
Gilliland et al. (2002)	12		2000	16.4	17.4	14.9	***
Gowen et al. (2003)	4		1999	19.1	19.2	18.8	ns
	4		2000	21.6	21.9	21.5	ns
Smit et al. (2005a)	6		2000	21.6	22.3	20.5	**
	6		2001	20.5	21.7	18.8	***
Smit et al. (2005b)	4		2002	17.4	18.0	16.4	***
	4		2003	15.1	15.9	14.3	***
Extended tiller height (cm)							
Gilliland et al. (2002)	12		2000	22.7	24.0	20.7	***
Smit et al. (2005a)	6		2000	28.5	30.9	24.6	*
	6		2001	27.7	29.7	26.2	ns
Smit et al. (2005b)	4		2002	23.8	25.3	21.4	**
	4		2003	19.7	21.2	18.2	***

Table 1 (cont.)

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Reference	Number of cvs.	Cutting height	Exp. year	Mean	Max.	Min.	Cultivar effects
Bulk density ($g\ DM\ cm^{-3}$)							
O'Donovan (2001)	4	4 cm	1999	1.52	1.65	1.40	***
	4		2000	1.42	1.47	1.34	***
Gilliland et al. (2002)	12	3 cm	2000	0.77	0.87	0.68	***
Smit et al. (2005a)	6	6 cm	2000	1.42	1.52	1.36	***
	6		2001	1.69	1.83	1.56	***
Smit et al. (2005b)	4	4 cm	2002	1.58	1.62	1.54	ns
	4		2003	2.06	2.10	2.02	ns
Tiller density ($tillers\ m^{-2}$)							
Orr et al. (2003)	15		1998	17268	24540	13220	***
	15		1999	25593	32540	20180	***
O'Donovan (2001)	4		1999	5272	6106	4411	***
	4		2000	5931	6634	4691	***
Smit et al. (2005a)	6		2000	5182	6166	4063	***
	6		2001	12995	15344	10872	**
Smit et al. (2005b)	4		2002	8077	8547	7061	**
	4		2003	9058	9438	8489	ns
Proportion of leaf blade ($g\ g^{-1}\ DM$)							
Gilliland et al. (2002)	12	3 cm	2000	0.84	0.91	0.75	***
Gowen et al. (2003)	4	4 cm	1999	0.61	0.65	0.57	*
	4		2000	0.64	0.68	0.62	*
Smit et al. (2005a)	6	6 cm	2000	0.83	0.88	0.79	***
	6		2001	0.80	0.84	0.75	***
Smit et al. (2005b)	4	4 cm	2002	0.77	0.78	0.76	ns
	4		2003	0.68	0.70	0.66	ns

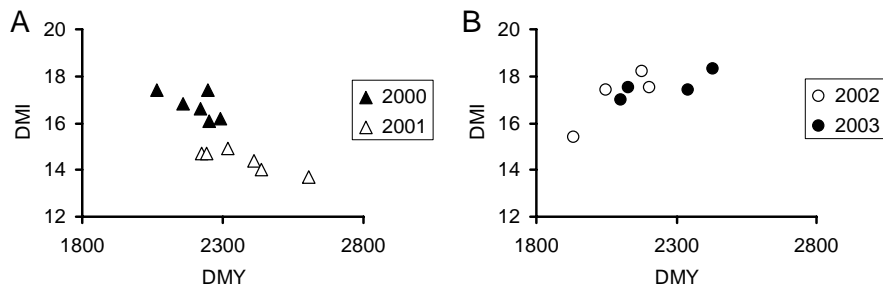


Figure 1. The relation between dry-matter yield (DMY) ($kg\ ha^{-1}$) and herbage intake (DMI) ($kg\ day^{-1}$) during stall feeding (A) and grazing (B)

In a grazing situation, DMY affects also herbage allowance and therefore plays a different role. When animals are offered more herbage, they will increase their intake. So, consumption will be higher in cultivars with a higher DMY. This mechanism will continue until the animal is saturated. Above 40 kg of available

herbage per animal, the herbage intake seemed not to increase anymore (Figure 1B) (Lantinga 1985; Minson 1987). A higher herbage allowance will give the animal more opportunities to select. So, although the digestibility of the total herbage might decrease, the consumed herbage might have a better quality in a situation with a higher herbage allowance.

Sward surface height

Sward surface height (SSH) can be expressed as compressed sward surface height (using a plate meter) or as extended tiller height (ETH) (using a ruler) (Gilliland et al. 2002; Smit et al. 2005a). SSH is one of the most important characteristics controlling bite mass and intake rate (Laca et al. 1992; Casey and Brereton 1999; McGilloway et al. 1999). Bite mass will increase with increasing sward surface height; however, intake rate will decrease in taller swards (Laca et al. 1992). Among perennial ryegrass cultivars, variation in SSH exists (Table 1). However, these differences were found in projects screening large numbers of perennial ryegrass cultivars. In studies with fewer cultivars (O'Donovan 2001; Barrett et al. 2003; Orr et al. 2005), no significant differences between the diploid cultivars were found. The differences in sward surface height were most prominent in spring and early summer, whereas in the vegetative stage they were generally not larger than 3-4 cm. The differences found under cutting were consisted with those under grazing (Smit 2005). Tetraploid cultivars might have a higher sward surface height than diploid cultivars (Gilliland et al. 2002).

Bulk and tiller density

Bulk density is the herbage mass (kg DM m^{-2}) divided by the sward surface height and expressed as kg DM per m^3 . A higher bulk density is associated with an increased bite mass in homogeneous swards (Laca et al. 1992; McGilloway et al. 1999). Especially when the sward height decreases, the relative importance of bulk density will increase (Casey and Brereton 1999). Bite volume will be smaller in denser swards (Casey and Brereton 1999). Differences among cultivars of perennial ryegrass for bulk density have been found in both cutting (Gilliland et al. 2002; Smit et al. 2005a) and grazing experiments (O'Donovan 2001).

A higher bulk density can be achieved by an increased tiller density (number of tillers m^{-2}) or by an increased tiller weight. In a two-year grazing experiment with dairy cattle by O'Donovan (2001), diploid cultivars always had a higher tiller density (6500 tillers m^{-2}) than tetraploids (4500 tillers m^{-2}). This observation was confirmed by Orr et al. (2003) in a grazing study with sheep, although with much higher tiller densities (24000 vs. 17000 tillers m^{-2}) due to the grazing of sheep, which promotes site filling. Also among diploid perennial-ryegrass cultivars variation in tiller density exists. Tiller density fluctuates during the season, but cultivars with an increased tiller density in spring usually maintain this during the season (Orr et al. 2003; Smit et al. 2005a). Cultivar differences in tiller weight have been found. However, the differences were minor (Smit et al. 2005a). Tiller weight was strongly negatively related with tiller density. This self-thinning principle is proposed by Yoda et al. (1963) and implies that densely populated swards contain

many small tillers, whereas more open swards contain fewer, but heavier tillers.

Morphology and green-leaf mass

During most of the year, the perennial-ryegrass plant is almost entirely composed of leaf tissue. In the vegetative growth stage, the canopy consists of leaf blades, pseudostems and dead material. In late spring, the reproductive tillers of the perennial ryegrass elongate and inflorescences are formed. The inflorescence grows on a stem that is lignified and can extend to 60 cm (Peeters 2005).

There are clear differences in the time of the year the perennial ryegrass cultivars start heading. Early heading cultivars start their heading stage half May, but very early cultivars heading in the beginning of May have been reported (Munro et al. 1992). Late heading cultivars start heading in June (Bonthuis et al. 2004). When cultivars were compared over the whole season, differences among cultivars were found for morphological parameters, e.g., leaf-blade proportion and (pseudo-)stem proportion, under cutting (Gilliland et al. 2002). Under grazing by dairy cows (Smit et al. 2005b), especially the pseudo-stem proportion differed among cultivars, but no cultivar effect was found for leaf-blade proportion.

Diploid cultivars tend to have a slightly lower leaf-blade proportion than tetraploids (3-4%) (O'Donovan 2001; Gilliland et al. 2002). Late heading cultivars were found to have a higher leaf-blade proportion than intermediate and early heading cultivars (O'Donovan 2001; Gilliland et al. 2002). The proportion of dead material can differ significantly among cultivars. This could be associated with the severity of a crown-rust infestation. The absolute level of dead material might be more associated with water availability (Smit et al. 2005b).

Green leaf mass is the product of herbage yield and the leaf-blade proportion. Perennial-ryegrass cultivars differ in their annual green-leaf mass (Gilliland et al. 2002; Orr et al. 2003; Smit et al. 2005b). Tetraploids are generally associated with a higher green-leaf mass (Gilliland et al. 2002; Hageman et al. 1992). However, in a grazing study with sheep (Orr et al. 2003) this effect of ploidy was not found. Green-leaf mass in the upper horizon of the sward (>10 cm) was found to be associated with a higher intake by sheep (Hazard et al. 1998). This positive relation was also found for grazing dairy cows (Smit et al. 2005b), but differences among cultivars for intake were not significant in this study. Orr et al. (2004) found a positive relation between bite mass of yearling dairy heifers and green-leaf mass when leaf/stem ratios were changing, but did not find this for grazing sheep.

Nutritive value

Nutritive value of herbage has become much more of the researchers' interest in the last decades. In an assessment among the world's leading nutritionists and breeders (Smith et al. 1997) of the relative importance of specific traits for genetic improvement of nutritive value of grasses, high digestibility, a high rate of digestion, increasing the non-structural carbohydrates content, and high palatability were listed numbers 1 to 4. For good future breeding perspectives, traits need to be significantly different among cultivars and consistent over a couple of experimental years (Casler

1998; Wilkins and Humphreys 2003).

Digestibility and rate of digestion

The cultivar effects on digestibility affect herbage intake and herbage utilization (Munro et al. 1992). *In vitro* digestibility is considered by some breeders to be not important in perennial ryegrass (Boller et al. 1994), because the level already is rather high (>75%), whereas others (Ingram and Beerepoot 1994) consider digestibility of great value. The potential financial impact of small improvements could be large, e.g., a 5 % increase in herbage digestibility could lead up to 100 euro ha⁻¹ for an average farmer. This premium is achieved by substitution of concentrate feed for grass (Vellinga and Van Loo 1994). *In vitro*-digestibility estimates, either by laboratory methods or near-infrared reflectance spectroscopy (NIRS), can often reveal differences in digestibility among cultivars more precisely, e.g., Tas (2005) could not confirm a small variation among cultivars in 2000 in *in vitro* digestibility with *in vivo* values in a stall-feeding situation. However, in 2001, when the variation of the *in vitro* digestibility was 6 %, a variation of 4 % among cultivars was demonstrated *in vivo*.

Perennial-ryegrass cultivars differ significantly and consistently for *in vitro* digestibility (Beerepoot and Agnew 1997; Orr et al. 2001; Smit 2005). The digestibility in the study of Smit (2005) had a variation of between 2 to 6 % among cultivars, as shown in Figure 2.

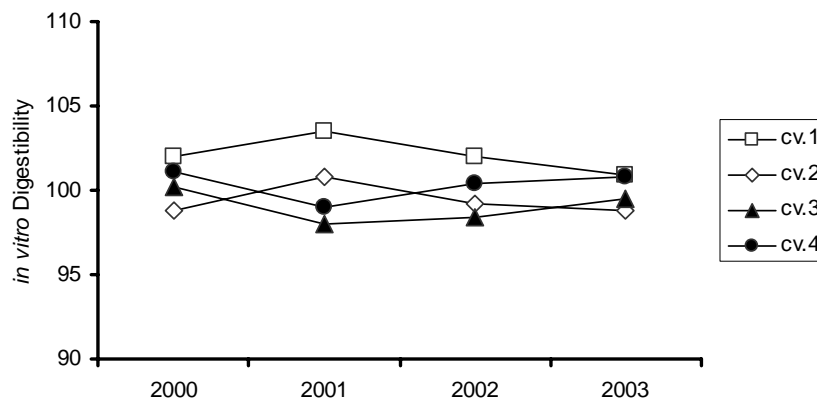


Figure 2. The variation in *in vitro* digestibility estimated by NIRS expressed as index figure to the annual mean (100) of four perennial-ryegrass cultivars (1. Abergold, 2. Agri, 3. Barezane and 4. Barnhem) during the four years

Water-soluble carbohydrates

It has long been known that ruminants prefer species with a high concentration of water-soluble carbohydrates (WSC) (Heady 1964). Humphreys (1989) showed that WSC concentration is a consistent and heritable trait, and that there are opportunities

to breed perennial-ryegrass cultivars with an increased WSC concentration. A variation of 20 % for WSC concentration among six diploid cultivars was found to be consistent over several years (Smit 2005), as shown in Figure 4A. The largest variation among cultivars was found during summer, in July and August. Tetraploid cultivars generally have a higher WSC concentration than diploid cultivars (Smith et al. 2001; Gilliland et al. 2002).

There is a general decline in WSC during the season, as shown in Figure 3. The lower WSC concentration in autumn has several causes. Firstly, the reduced solar radiation will decrease photosynthetic activity, which results in a reduced primary production of non-structural carbohydrates. It has been shown (Fulkerson and Donaghy 2001) that WSC concentrations are closely related with hours of sunlight. There is a general increase in WSC concentration in the upper part of the sward (the area with most photosynthetic activity) during the day (Delagarde et al. 2000; Smit and Elgersma 2004). Furthermore, pasture plants respire and use the produced WSC. If the amount of WSC is inadequate (e.g., during night time or cloudy weather), also the non-structural carbohydrate reserves are used (Fulkerson and Donaghy 2001). The higher night temperatures in autumn will induce respiration during night time (McGrath 1988). The altering source – sink relations deplete WSC reserves, and hence lower the WSC concentration in the herbage.

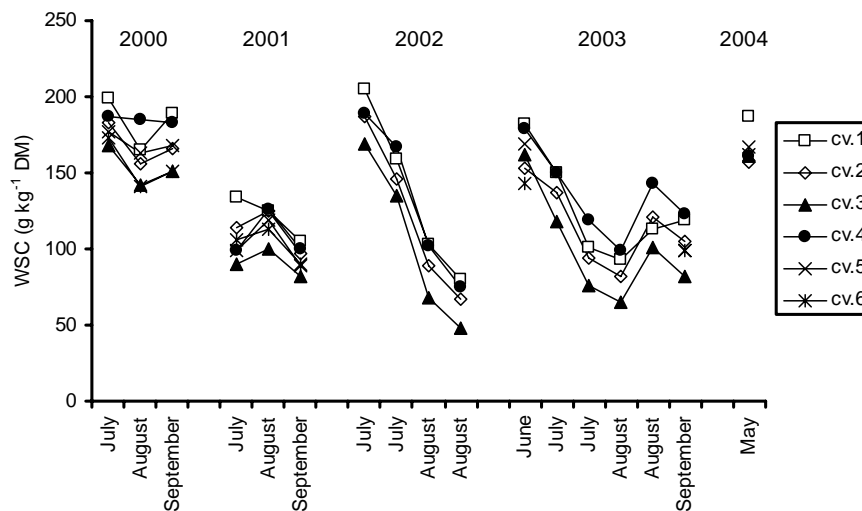


Figure 3. WSC concentrations (g kg^{-1} DM) of six perennial-ryegrass cultivars (1. Abergold, 2. Agri, 3. Barezane, 4. Barnhem, 5. Herbie and 6. Respect) during four years (Tas et al. 2005; Smit et al. 2005b)

Fibres

Feed intake by ruminants is mainly controlled by physical factors, such as the cow's rumen holding capacity (rumen fill) for DM or fibre. Fibres in grasses mainly

consist of cellulose, hemicellulose and lignin. In a 4-year comparison of four *Lolium perenne* cultivars (Smit 2005), variation (7-15 %) was found in lignin concentration (Figure 4B). The variation in NDF content was much less and not very consistent (Figure 4C). Lantinga et al. (1996) suggested that perennial-ryegrass varieties might differ in their cell-wall degradation rates. However, Taweel (2004) tested this hypothesis and reported that variation in fermentation characteristics within perennial-ryegrass varieties was mainly due to variation in the rapidly fermentable fraction, and that fermentation characteristics of the slowly fermentable fraction were not different among the grass varieties tested. Moreover, based on the results of an *in vivo* rumen evacuation experiment, Taweel et al. (2005) reported that selecting for fast degrading fibre seemed to be beneficial in improving DMI, fibre utilization and milk yield, but breeding potential within perennial-ryegrass cultivars appeared to be very limited as a very small range was observed. The difference in fractional degradation rate between the variety with the fastest degrading fibre and the one with the slowest degrading fibre was less than 1 %/h.

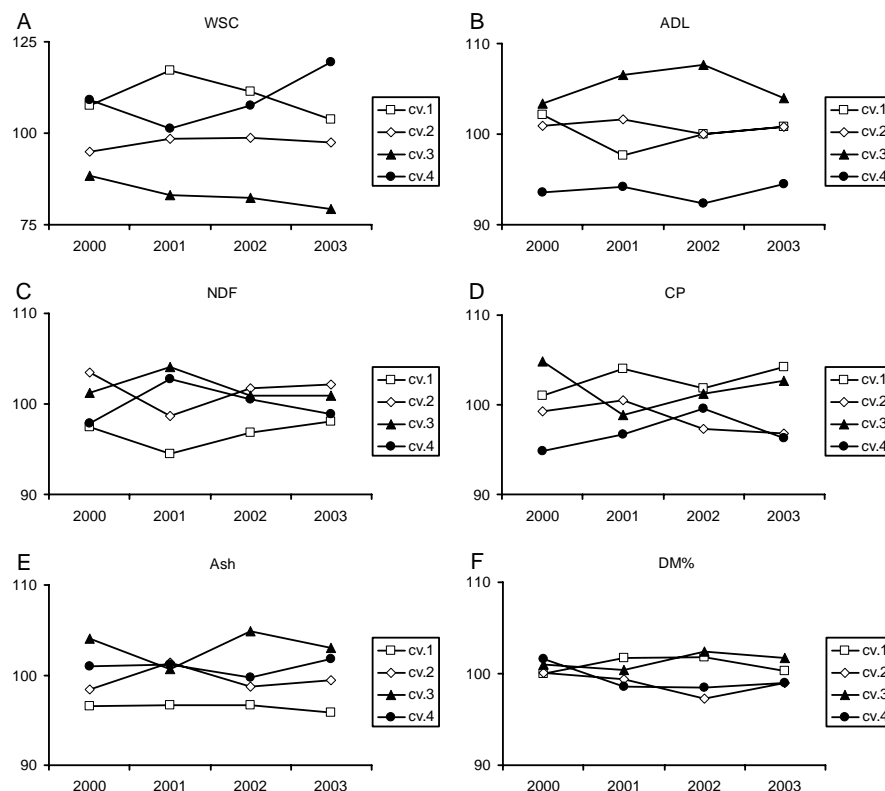


Figure 4. The variation in (A) water-soluble carbohydrates (WSC); (B) acid detergent lignin (ADL); (C) neutral detergent fibre (NDF); (D) crude protein (CP); (E) ash and (F) dry-

matter concentration (DM %), expressed as index figure to the annual mean (100) of four perennial-ryegrass cultivars (1. Abergold, 2. Agri, 3. Barezane and 4. Barnhem) during the four years (values taken from Tas et al. 2005; Smit et al. 2005b)

Protein

Improving yields of herbage by breeding without applying more nitrogen fertilizer is one of the ways to be less polluting and decrease costs at the same time (Vellinga and Van Loo 1994). During the last decades much effort has been put in improving in the nitrogen use efficiency in grasses (Casler and Vogel 1999). Much improvement has been achieved (Vellinga and Andre 1999), which is partly attributable to genetic improvement of the cultivars, but also to improved grassland management.

The ranking order of cultivars remains similar for annual yield of DM and N with increasing fertilizer levels (Wilkins et al. 2000), implying that there is hardly any genotype – environment interaction. Therefore, high-performing cultivars will also perform better under situations with a low nitrogen availability.

Smit (2005) found a small, but significant variation in nitrogen concentration among cultivars of perennial ryegrass (Figure 4D). Breeding for an increased nitrogen concentration was related with a greater proportion of leaves (Hazard et al. 1998; Bélanger et al. 2001). Most photosynthesis is carried out in the leaves, explaining their high protein content. The nitrogen content is higher in young leaves at the upper part of the sward than in the older leaves lower in the sward (Delagarde et al. 2000; Smit and Elgersma 2004). The nitrogen content in leaves has also been found to differ among perennial-ryegrass cultivars. This, however, was negatively related with yield of DM and N (Wilkins et al. 2000; Bélanger et al. 2001), leading to the hypothesis that the metabolic cost of protein synthesis and turnover are the key factors controlling genetic variation both in leaf yield and annual DM and N yield. Seasonal variation in herbage protein concentration was much larger than the differences among cultivars. In May, the period of the blooming of the grass, herbage protein levels usually drop below minimum required level in a dairy cows' diet of 125 g kg⁻¹ DM, whereas the levels in early spring and late summer are usually much higher (Wilkins et al. 2000).

Physical characteristics

Toughness of leaves and their component tissues is of biological significance, playing a major role in the resistance of leaves to herbivores, pathogens and other physical damage (Choong et al. 1992). Tough leaves could be avoided by herbivores because of higher energetic expenses for harvesting, but also because of a lower palatability (Wright and Vincent 1996). Naturally this information is of use to the plant breeder who can select for important characteristics (Vincent 1982). Of more fundamental importance is the fact that from a mechanical point of view, grass is probably the simplest of all plants and is therefore a good starting point to understand the mechanical properties of plants (Vincent 1982). Smit (2005) examined six perennial ryegrass cultivars for their tensile-breaking force (N), as

described by Henry et al. (1997) but using the conventional clamps as described by Theron and De Booysen (1968) and the Zwick apparatus (Z2.5, Zwick, Ulm, Germany). In three years the maximal breaking force was measured and the results are shown in Table 2. In all years Abergold had the lowest and Agri had always the highest breaking force. Tensile strength parameters might be better expressed as N mm⁻² (Vincent 1982; 1991) (MacAdam and Mayland 2003). Leaf tensile strength was related to the width of the leaf ($P < 0.001$, $R^2 = 0.72$). Further research should investigate whether the leaf tensile properties also differ among cultivars when expressed in relation to their transverse leaf blade area.

Table 2. The maximum breaking force (N), tested among six perennial-ryegrass cultivars (taken from Smit 2005)

Year	Cultivar						s.e.d.
	Abergold	Agri	Barezane	Barnhem	Herbie	Respect	
2000	5.6	7.1	6.0	6.0	6.3	6.6	0.45
2001	6.5 ^a	7.8 ^d	6.9 ^{abc}	6.7 ^{ab}	7.1 ^{bc}	7.4 ^{cd}	0.27
2002	7.8	8.5	8.3	8.6			0.36

^{a,b,c} means within the same row followed by the same subscript are not significantly different ($P > 0.05$).

Table 3. Proportion of leaves severely infested by crown rust (*Puccinia coronata* f. sp. *lolii*) of six perennial-ryegrass cultivars (taken from Smit 2005)

Year	Cultivar						s.e.d
	Abergold	Agri	Barezane	Barnhem	Herbie	Respect	
2000	9.5 ^a	14.0 ^b	20.1 ^c	5.3 ^a	17.2 ^{bc}	15.4 ^b	6.6
2001	No data recorded*						
2002	13.8 ^a	27.1 ^b	40.9 ^c	11.8 ^a			3.7
2003	7.8 ^a	12.1 ^a	21.9 ^b	4.9 ^a			4.4

*In 2001, no data were recorded. The visual impression was that no crown-rust infestation occurred.

^{a,b,c} means within the same row followed by the same subscript are not significantly different ($P > 0.05$).

Disease resistance

Infestation of crown rust mainly takes place during humid, warm weather and in situations of reduced growth. In autumn, the growing conditions for the fungi are favourable. The effects of crown rust on palatability are not well described in the literature, but it is generally accepted that animals do not like to eat infested herbage, because of a bitter taste (Potter 1987; Tas 2005). As shown in Table 3, there was a large variation in resistance among diploid cultivars of perennial ryegrass. In all experimental years, two cultivars (Abergold and Barnhem) were least infested by the fungi, whereas Barezane was most infested (Table 3). In this study no complete

resistance was found as even in the most resistant cultivar spots of crown rust were found, especially in periods of reduced growth rates (in autumn or dry conditions in 2002 and 2003). In the past, cultivars with a high WSC concentration were reported to be more susceptible to crown-rust infestations (Smith et al. 1998). However, this was not found in this study, where the newer cultivars (Abergold and Barnhem) both had a higher WSC concentration and were less susceptible to crown rust (Smit et al. 2005b). The resistance could further be improved, by conventional selection or by using molecular-marker techniques (Reheul and Ghesquiere 1996; Smith et al. 1998; Kimbeng 1999).

EFFECTS OF PERENNIAL RYEGRASS ON HERBAGE INTAKE DURING GRAZING

Preference and palatability

Large herbivores are generally considered bulk feeders, but they also have their preferences (Heady 1964). Preference behaviour among different forage species is a well recognized and frequently studied concept (Heady 1964; Belovsky 1978; Stephens and Krebs 1986; Rutter et al. 2002). Species that are less abundant are generally highly selected or rejected, while abundant species, in most cases grasses, furnish the bulk of the diet (Van Dyne and Heady 1965). In modern agriculture, however, cultivated pastures in the temperate climate zones have become completely dominated by grasses, sometimes of only a single species.

In several grass species, cattle showed preference among cultivars, e.g., in tall fescue (*Festuca arundinacea*) (Shewmaker et al. 1997), annual ryegrass (*Lolium multiflorum*) (Aderibigbe et al. 1982) and perennial ryegrass (*Lolium perenne*) (O'Riordan et al. 1998; Smit 2005). Simon and Daniel (1983) concluded for sheep and O'Riordan et al. (1998) for cattle, that tetraploid cultivars were preferred over diploid cultivars of perennial ryegrass. Jones and Roberts (1991) and Hazard et al. (1998) reported that sheep selected among four diploid perennial-ryegrass cultivars and concluded that cultivars with a high WSC concentration were preferred. In dairy cattle this was also found by Smit (2005); dairy cattle that had access to six cultivars consistently preferred the cultivars with a high WSC concentration, high digestibility and low ash and NDF concentration. Literature suggests that WSC increases palatability (Heady 1964; Jones and Roberts 1991; Mayland et al. 2000b), but no relation could be made with specific components, e.g., malate or citrate (Mayland et al. 2000a). Others (Van Vuuren 1993; Taweel 2004) pointed to the effect that feeding cultivars with elevated WSC concentrations lowers the $\text{NH}_3\text{-N}$ concentration in the rumen. The $\text{NH}_3\text{-N}$ concentration in the rumen could play a role in long-term diet selection (Kyriazakis and Oldham 1997). Still, the question remains why dairy cows do select for high-sugar cultivars. This needs further examination.

Intake characteristics

In several studies in the last decade, the effect of perennial-ryegrass cultivars on

herbage intake characteristics has been investigated (Munro et al. 1992; Hazard et al. 1998; Casey and Brereton 1999; Gowen et al. 2003; Orr et al. 2003; Barrett et al. 2003; Orr et al. 2005; Smit et al. 2005b; Tas et al. 2005). The intake of herbage by grazing herbivores could be divided into several characteristics that are important: daily intake, intake rate, bite mass, bite number or biting time and bite volume.

Studies with sheep (Munro et al. 1992; Hazard et al. 1998; Orr et al. 2003) have shown that perennial-ryegrass cultivars can have effects on sheep. Munro et al. (1992) showed a large effect of one cultivar (cv. Aurora) compared to others on lamb live-weight production, most likely caused by an increased intake and a better digestibility of this cultivar. Hazard et al. (1998) showed differences among four perennial-ryegrass cultivars in daily intake by stall-fed sheep and indicated green-leaf mass as a potential trait for breeding. Orr et al. (2003) showed an effect of cultivars on both daily intake and intake rate in 15 intermediate-heading perennial-ryegrass cultivars, but could not identify clear relations with plant characteristics related to this increased intake.

The effects of perennial-ryegrass cultivars on cattle are less straightforward. The variation among perennial-ryegrass cultivars that was found for several characteristics was clearly insufficient to have a large effect on dairy cows' performance (Smit 2005). However, in dairy cows differences have been found between diploid and tetraploid cultivars (Hageman et al. 1992) showing that tetraploid cultivars have a high potential for grazing animals, such as a higher water-soluble carbohydrates level, and a high green-leaf mass (GLM). Cultivar differences in bulk density have reported to affect bite mass of dairy cows (Casey and Brereton 1999). Barrett et al. (2003), however, found only cultivar effects on bite depth and not on bite mass and other intake characteristics by dairy cows using four of the six ryegrass cultivars used by Casey and Brereton (1999). Gowen et al. (2003) found an effect on daily intake by grazing dairy cows and showed that late-heading perennial-ryegrass cultivars might have better potential than intermediate-heading cultivars. Orr et al. (2005) did not find differences in grazing beef cattle among four perennial-ryegrass cultivars for any behavioural aspects, such as intake rate, biting rate, chewing rate and total jaw movement rate. Lee et al. (2002) found an effect on intake of growing steers of a cultivar with increased water-soluble-carbohydrates concentration. In contrast, no effects of these cultivars on DMI by dairy cows were found by Miller et al. (2001). Variation among cultivars in sward structural components and chemical composition did not lead to a higher herbage intake by dairy cows when fed a single cultivar, neither in a stall-feeding (Tas et al. 2005) nor in a grazing situation (Smit et al. 2005b). In this last experiment, only in 2002 a significant cultivar effect on herbage intake was observed, but this was probably due to a severe crown-rust infestation in the most susceptible cultivar (Barezane). The reduction of herbage intake could, however, not clearly be pinpointed to crown rust alone. Cultivar Barezane had in the same year also a lower SSH, DMY, GLM and WSC concentration and a higher ADL concentration than the other cultivars. In 2003, however, the same cultivar had again a lower SSH, DMY, GLM and WSC concentration and a higher ADL concentration, but in this year the crown-rust infestation was less severe and no cultivar effects on herbage intake were found. The main cause of the reduced herbage intake is therefore thought to be the crown-rust

infestation.

BREEDING CULTIVARS FOR INCREASED HERBAGE INTAKE

From this review it should be clear that there are differences among diploid cultivars of perennial ryegrass for yield, sward structural and morphological characteristics, and concentrations of water-soluble carbohydrates and lignin. These results show promising objectives for breeding cultivars for a specific trait. Differences in other chemical components, crude protein, neutral detergent fibre, and ash, were minor.

Dairy cows showed a clear preference for the cultivars with an increased WSC concentration and digestibility and a decreased NDF and ash concentration. So breeding can have a role in creating cultivars that are preferred, which might play a role in composing seed mixtures.

The possibilities to enhance dry-matter intake in a grazing situation through breeding can mainly be achieved by a better crown-rust resistance and a higher dry-matter production. A higher dry-matter production would give more opportunities for selection by dairy cows and might, therefore, enhance herbage intake on animal level. The production of more herbage would certainly enhance herbage intake on a farm level.

REFERENCES

- Aderibigbe, A.O., Church, D.C., Frakes, R.V., et al., 1982. Factors determining palatability of ryegrass to cattle. *Journal of Animal Science*, 54 (1), 164-172.
- Barrett, P.D., McGilloway, D.A., Laidlaw, A.S., et al., 2003. The effect of sward structure as influenced by ryegrass genotype on bite dimensions and short-term intake rate by dairy cows. *Grass and Forage Science*, 58 (1), 2-11.
- Beerepoot, L.J. and Agnew, R.E., 1997. Breeding for improved herbage quality in perennial ryegrass. In: *Seeds of progress: proceedings of the BGS/BSPB/NIAB/SAC Conference, Nottingham, UK, 18-19 February 1997*. British Grassland Society, Reading, 135-145. BGS Occasional Symposium no. 31.
- Beever, D.E., Offer, N. and Gill, E.M., 2000. The feeding value of grass and grass products. In: Hopkins, A. ed. *Grass its production and utilization*. 3rd edn. Blackwell Science, Oxford, 140-195.
- Bélanger, G., Michaud, R., Jefferson, P.G., et al., 2001. Improving the nutritive value of timothy through management and breeding. *Canadian Journal of Plant Science*, 81 (4), 577-585.
- Belovsky, G.E., 1978. Diet optimization in a generalist herbivore: the moose. *Theoretical Population Biology*, 14 (1), 105-134.
- Boller, B., Turner, R. and Van Loo, E.N., 1994. Report of Workshop 2. In: Reheul, D. and Ghesquiere, A. eds. *Breeding for quality: proceedings of the 19th EUCARPIA Fodder Crops Section Meeting held in Brugge, Belgium, 5-8 October 1994*. EUCARPIA, Wageningen.
- Bonthuis, H., Donner, D.A. and Van Vliegen, A., 2004. *79ste rassenlijst voor landbouwgewassen*. Plant Research International, Wageningen.
- Casey, I.A. and Brereton, A.J., 1999. *Optimising sward structure and herbage yield for performance of dairy cows at pasture*. Teagasc, Fermoy. Teagasc Report no. 4170. [<http://www.teagasc.ie/research/reports/dairyproduction/4170/eopr-4170.pdf>]
- Casler, M.D., 1998. Breeding cool-season grasses. In: Cherney, J.H. and Cherney, D.J.R. eds. *Grass for dairy cattle*. CAB International., Wallingford, 23-47.
- Casler, M.D. and Vogel, K.P., 1999. Accomplishments and impact from breeding for increased forage nutritional value. *Crop Science*, 39 (1), 12-20.

- Chilibroste, P., 1999. *Grazing time: the missing link: a study of the plant-animal interface by integration of experimental and modelling approaches*. PhD Thesis, Wageningen University, Wageningen.
- Choong, M.F., Lucas, P.W., Ong, J.S.Y., et al., 1992. Leaf fracture-toughness and sclerophylly: their correlations and ecological implications. *New Phytologist*, 121 (4), 597-610.
- De Vries, D.M., 't Hart, M.L. and Kruijne, A.A., 1942. Een waardering van grasland op grond van de plantkundige samenstelling. *Landbouwkundig Tijdschrift*, 54 (663), 245-265.
- Delagarde, R., Peyraud, J.L., Delaby, L., et al., 2000. Vertical distribution of biomass, chemical composition and pepsin-cellulase digestibility in a perennial ryegrass sward: interaction with month of year, regrowth age and time of day. *Animal Feed Science and Technology*, 84 (1/2), 49-68.
- Fulkerson, W.J. and Donaghy, D.J., 2001. Plant-soluble carbohydrate reserves and senescence: key criteria for developing an effective grazing management system for ryegrass-based pastures: a review. *Australian Journal of Experimental Agriculture*, 41 (2), 261-275.
- Gilliland, T.J., Barrett, P.D., Mann, R.L., et al., 2002. Canopy morphology and nutritional quality traits as potential grazing value indicators for *Lolium perenne* varieties. *Journal of Agricultural Science*, 139 (3), 257-273.
- Gowen, N., O'Donovan, M., Casey, I., et al., 2003. The effect of grass cultivars differing in heading date and ploidy on the performance and dry matter intake of spring calving dairy cows at pasture. *Animal Research*, 52 (4), 321-336.
- Hageman, I.W., Lantinga, E.A. and Schlepers, H., 1992. *Opname, voederwaarde, melkproductie en zodekwaliteit bij beweiding van diploid en tetraloid Engels Raaigras: verslag van een tweejarig vergelijkend onderzoek*. Landbouwniversiteit, Vakgroep Landbouwplantenteelt en Graslandkunde, Wageningen.
- Hazard, L., De Moraes, A., Betin, M., et al., 1998. Perennial ryegrass cultivar effects on intake of grazing sheep and feeding value. *Annales de Zootechnie*, 47 (2), 117-125.
- Heady, H.F., 1964. Palatability of herbage and animal preference. *Journal of Rangeland Management*, 17 (2), 76-82. [<http://jrm.library.arizona.edu/data/1964/172/6head.pdf>]
- Henry, D.A., Simpson, R.J. and Macmillan, R.H., 1997. Intrinsic shear strength of leaves of pasture grasses and legumes. *Australian Journal of Agricultural Research*, 48 (5), 667-674.
- Humphreys, M.O., 1989. Water-soluble carbohydrates in perennial ryegrass breeding. III. Relationships with herbage production, digestibility and crude protein content. *Grass and Forage Science*, 44 (4), 423-429.
- Ingram, J. and Beerepoot, L.J., 1994. Report of Workshop 1. In: Reheul, D. and Ghesquiere, A. eds. *Breeding for quality: proceedings of the 19th EUCARPIA Fodder Crops Section Meeting held in Brugge, Belgium, 5-8 October 1994*. EUCARPIA, Wageningen.
- Jones, E. L. and Roberts, J. E., 1991. A note on the relationship between palatability and water-soluble carbohydrates content in perennial ryegrass. *Irish Journal of Agricultural Research*, 30 (2), 163-167.
- Kimbeng, C.A., 1999. Genetic basis of crown rust resistance in perennial ryegrass, breeding strategies, and genetic variation among pathogen populations: a review. *Australian Journal of Experimental Agriculture*, 39 (3), 361-378.
- Kyriazakis, I. and Oldham, J.D., 1997. Food intake and diet selection in sheep: the effect of manipulating the rates of digestion of carbohydrates and protein of the foods offered as a choice. *British Journal of Nutrition*, 77 (2), 243-254.
- Laca, E.A., Ungar, E.D., Seligman, N., et al., 1992. Effects of sward height and bulk density on bite dimensions of cattle grazing homogeneous swards. *Grass and Forage Science*, 47 (1), 91-102.
- Laidlaw, A.S. and Reed, K.F.M., 1993. Plant improvement: the evaluation and extension process. In: Baker, M.J. ed. *Grasslands for our world: proceedings of the 17th international grassland congress, held in February 1993, in New Zealand and Queensland*. SIR, Wellington, 385-392.
- Lantinga, E.A., 1985. *Productivity of grasslands under continuous and rotational grazing*. PhD Thesis, Wageningen Agricultural University, Wageningen.
- Lantinga, E.A. and Groot, J.C.J., 1996. Optimisation of grassland production and herbage feed quality in an ecological context. In: Groen, A.F. and Van Bruchem, J. eds. *Utilization of local feed resources by dairy cattle: perspectives of environmentally balanced production systems: symposium proceedings Wageningen Institute of Animal Sciences (WIAS), Wageningen, The Netherlands, 29 September 1995*. Wageningen Pers, Wageningen, 58-66. EAAP Publication no. 84.
- Lee, M.R.F., Harris, L.J., Moorby, J.M., et al., 2002. Rumen metabolism and nitrogen flow to the small intestine in steers offered *Lolium perenne* containing different levels of water-soluble carbohydrate. *Animal Science*, 74 (3), 587-596.

- MacAdam, J.W. and Mayland, H.F., 2003. The relationship of leaf strength to cattle preference in tall fescue cultivars. *Agronomy Journal*, 95 (2), 414-419.
- Mayland, H.F., Martin, S.A., Lee, J.L., et al., 2000a. Malate, citrate, and amino acids in tall fescue cultivars: relationship to animal preference. *Agronomy Journal*, 92 (2), 206-210.
- Mayland, H.F., Shewmaker, G.E., Harrison, P.A., et al., 2000b. Nonstructural carbohydrates in tall fescue cultivars: relationship to animal preference. *Agronomy Journal*, 92 (6), 1203-1206.
- McGilloway, D.A., Cushnahan, A., Laidlaw, A.S., et al., 1999. The relationship between level of sward height reduction in a rotationally grazed sward and short-term intake rates of dairy cows. *Grass and Forage Science*, 54 (2), 116-126.
- McGrath, D., 1988. Seasonal variation in the water-soluble carbohydrates of perennial and Italian ryegrass under cutting conditions. *Irish Journal of Agricultural Research*, 27 (2/3), 131-139.
- Meijs, J.A.C., 1981. *Herbage intake by grazing dairy cows*. PUDOC, PhD Thesis Wageningen University, Wageningen. Agricultural Research Reports no. 909.
- Miller, L.A., Moorby, J.M., Davies, D.R., et al., 2001. Increased concentration of water-soluble carbohydrate in perennial ryegrass (*Lolium perenne*): milk production from late-lactation dairy cows. *Grass and Forage Science*, 56 (4), 383-394.
- Minson, D.J., 1987. Plant factors affecting intake. In: Snaydon, R.W. ed. *Ecosystems of the world. 17B. Managed grasslands analytical studies*. Elsevier, Amsterdam, 137-144.
- Munro, J.M.M., Davies, D.A., Evans, W.B., et al., 1992. Animal production evaluation of herbage varieties. 1. Comparison of Aurora with Frances, Talbot and Melle perennial ryegrass when grown alone and with clover. *Grass and Forage Science*, 47 (3), 259-273.
- Neuteboom, J.H., 1986. Landbouwkundige waardering en ecologie van graslandplanten. *Gebundelde Vrslagen van de Nederlandse Vereniging voor Weide- en Voederbouw*, 27, 15-24.
- O'Donovan, M., 2001. *The influence of grass cultivars on milk production*. Teagasc, Fermoy. Teagasc Report no. ARMIS-4572.
- O'Riordan, E.G., O'Kiely, P. and Keane, M.G., 1998. *Efficient beef production from grazed pasture*. Teagasc, Fermoy. Teagasc Report no. 4281. [<http://www.teagasc.ie/research/reports/beef/4281/eopr-4281.pdf>]
- Orr, R.J., Cook, J.E., Champion, R.A., et al., 2003. Intake characteristics of perennial ryegrass varieties when grazed by sheep under continuous stocking management. *Euphytica*, 134 (3), 247-260.
- Orr, R.J., Cook, J.E., Young, K.L., et al., 2005. Intake characteristics of perennial ryegrass varieties when grazed by yearling beef cattle under rotational grazing management. *Grass and Forage Science*, 60 (2), 157-167.
- Orr, R.J., Martyn, T.M. and Clements, R.O., 2001. Evaluation of perennial ryegrass varieties under frequent cutting or continuous stocking with sheep. *Plant Varieties and Seeds*, 14 (3), 181-199.
- Orr, R.J., Rutter, S.M., Yarrow, N.H., et al., 2004. Changes in ingestive behaviour of yearling dairy heifers due to changes in sward state during grazing down of rotationally stocked ryegrass or white clover pastures. *Applied Animal Behaviour Science*, 87 (3/4), 205-222.
- Peeters, A., 2005. *Lolium perenne L.* FAO, Rome. [<http://www.fao.org/ag/agp/agpc/doc/gbase/data/pf000449.htm>]
- Potter, L.R., 1987. Effect of crown rust on regrowth, competitive ability and nutritional quality of perennial and Italian ryegrasses. *Plant Pathology*, 36 (4), 455-461.
- Reheul, D. and Ghesquiere, A., 1996. Breeding perennial ryegrass with better crown rust resistance. *Plant Breeding*, 115 (6), 465-469.
- Rutter, S.M., Orr, R.J., Penning, P.D., et al., 2002. Ingestive behaviour of heifers grazing monocultures of ryegrass or white clover. *Applied Animal Behaviour Science*, 76 (1), 1-9.
- Shewmaker, G.E., Mayland, H.F. and Hansen, S.B., 1997. Cattle grazing preference among eight endophyte-free tall fescue cultivars. *Agronomy Journal*, 89 (4), 695-701.
- Simon, U. and Daniel, P., 1983. Effect of experimental methods on results of voluntary-intake experiments with grass cultivars. In: Smith, A.J. and Hay, V.W. eds. *Proceedings of the XIV International Grassland Congress, held at Lexington, Kentucky, USA, June 15-24, 1981*. Westview Press, Boulder, 489-491.
- Smit, H.J., 2005. *Perennial ryegrass for dairy cows: effects of cultivar on herbage intake during grazing*. PhD Thesis, Wageningen University, Wageningen.
- Smit, H.J. and Elgersma, A., 2004. Diurnal fluctuations in vertical distribution of chemical composition in a perennial ryegrass (*Lolium perenne L.*) sward during the season. In: Lüscher, A., Jeangros, B., Kessler, W., et al. eds. *Land use systems in grassland dominated regions: proceedings of the 20th*

- general meeting of the European Grassland Federation, Luzern, Switzerland, 21-24 June 2004.* Hochschulverlag AG an der ETH Zurich, Zurich, 951-953.
- Smit, H.J., Tas, B.M., Taweel, H.Z., et al., 2005a. Sward characteristics important for intake in six *Lolium perenne* varieties. *Grass and Forage Science*, 60 (2), 128-135.
- Smit, H.J., Tas, B.M., Taweel, H.Z., et al., 2005b. Effects of perennial ryegrass (*Lolium perenne* L.) cultivars on herbage production, nutritional quality and herbage intake of grazing dairy cows. *Grass and Forage Science*, 60 (3), 297-309.
- Smith, K.F., Reed, K.F.M. and Foot, J.Z., 1997. An assessment of the relative importance of specific traits for the genetic improvement of nutritive value in dairy pasture. *Grass and Forage Science*, 52 (2), 167-175.
- Smith, K.F., Simpson, R.J., Culvenor, R.A., et al., 2001. The effects of ploidy and a phenotype conferring a high water-soluble carbohydrate concentration on carbohydrate accumulation, nutritive value and morphology of perennial ryegrass (*Lolium perenne* L.). *Journal of Agricultural Science*, 136 (1), 65-74.
- Smith, K.F., Simpson, R.J., Oram, R.N., et al., 1998. Seasonal variation in the herbage yield and nutritive value of perennial ryegrass (*Lolium perenne* L.) cultivars with high or normal herbage water-soluble carbohydrate concentrations grown in three contrasting Australian dairy environments. *Australian Journal of Experimental Agriculture*, 38 (8), 821-830.
- Stephens, D.W. and Krebs, J.R., 1986. *Foraging theory*. Princeton University Press, Princeton.
- Tas, B.M., 2005. *Perennial ryegrass for dairy cows: intake, milk production and nitrogen utilisation*. PhD Thesis, Wageningen Universiteit, Wageningen.
- Tas, B.M., Taweel, H.Z., Smit, H.J., et al., 2005. Effects of perennial ryegrass cultivars on intake, digestibility, and milk yield in dairy cows. *Journal of Dairy Science*, 88 (9), 3240-3248.
- Taweel, H.Z., Tas, B.M., Smit, H.J., et al., 2005. Improving the quality of perennial ryegrass (*Lolium perenne* L.) for dairy cows by selecting for fast clearing and/or degradable neutral detergent fiber. *Livestock Production Science*, 96 (2/3), 239-248.
- Taweel, H.Z.H., 2004. *Perennial ryegrass for dairy cows: grazing behaviour, intake, rumen function and performance*. PhD Thesis, Wageningen University, Wageningen.
- Theron, E.P. and De Booysen, P.V., 1968. The tensile properties of ten indigenous grasses. *Proceedings of the Grassland Society of South Africa*, 3, 57-61.
- Van Dyne, G.M. and Heady, H.F., 1965. Botanical composition of sheep and cattle diets on a mature annual range. *Hilgardia*, 36 (13), 465-492.
- Van Vuuren, A.M., 1993. *Digestion and nitrogen metabolism of grass fed dairy cows*. PhD Thesis, Wageningen University, Wageningen.
- Van Wijk, A.J.P., Boonman, J.G. and Rumball, W., 1993. Achievements and perspectives in the breeding of forage grasses and legumes. In: Baker, M.J. ed. *Grasslands for our world: proceedings of the 17th international grassland congress, held in February 1993, in New Zealand and Queensland*. SIR, Wellington, 379-383.
- Van Wijk, A.J.P. and Reheul, D., 1991. Achievements in fodder crops breeding in maritime Europe. In: Den Nijs, A.P.M. and Elgersma, A. eds. *Fodder crops breeding: achievements, novel strategies and biotechnology: proceedings of the 16th meeting of the Fodder Crops Section of Eucarpia, Wageningen, Netherlands, 18-22 November 1990*. Pudoc, Wageningen, 13-18.
- Vellinga, T.V. and Andre, G., 1999. Sixty years of Dutch nitrogen fertiliser experiments, an overview of the effects of soil type, fertiliser input, management and of developments in time. *Netherlands Journal of Agricultural Science*, 47 (3/4), 215-241.
- Vellinga, T.V. and Van Loo, E.N., 1994. *Perspectieven grassenveredeling voor bedrijfsinkomen en mineralenoverschotten*. Proefstation voor de Rundveehouderij, Schapenhouderij en Paardenhouderij, Lelystad. Rapport / Proefstation voor de Rundveehouderij, Schapenhouderij en Paardenhouderij no. 151.
- Vincent, J.F.V., 1982. The mechanical design of grass. *Journal of Materials Science*, 17 (3), 856-860.
- Vincent, J.F.V., 1991. Strength and fracture of grasses. *Journal of Materials Science*, 26 (7), 1947-1950.
- Visser, J., 1998. Ontwikkelingen bij het rassenonderzoek. *Praktijkonderzoek / Praktijkonderzoek Rundvee, Schapen en Paarden (PR)*, 11 (2), 43-45.
- Wilkins, P.W., Allen, D.K. and Mytton, L.R., 2000. Differences in the nitrogen use efficiency of perennial ryegrass varieties under simulated rotational grazing and their effects on nitrogen recovery and herbage nitrogen content. *Grass and Forage Science*, 55 (1), 69-76.

- Wilkins, P.W. and Humphreys, M.O., 2003. Progress in breeding perennial forage grasses for temperate agriculture. *Journal of Agricultural Science*, 140 (2), 129-150.
- Wright, W. and Vincent, J.F.V., 1996. Herbivory and the mechanics of fracture in plants. *Biological Reviews of the Cambridge Philosophical Society*, 71 (3), 401-413.
- Yoda, K., Kira, T., Ogawa, H., et al., 1963. Intraspecific competition among higher plants. XI. Self-thinning in overcrowded pure stands under cultivated and natural conditions. *Journal of Osaka City University, Institute of Polytechnics. Series D. Biology*, 14, 107-129.