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Clover as a cover crop for weed suppression in an intercropping design I. Characteristics of several clover species

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Abstract

Weeds often form a major problem in weakly competitive vegetable crops, particularly in low input systems. Undersown cover crops can be used to suppress weeds, but often put too high a competitive pressure on the main crop. Cover crop selection is one of the potential means that can be used to design or optimize these intercropping systems. The objective of the current research was to investigate the variability among a range of clover species in morphological and physiological traits that are considered relevant for interplant competition. To this purpose, field experiments with pure stands of eight clover species (2001) and a selection of three clover species (2002) were conducted, in which regular observations and periodic harvests were taken. Clear differences in the time in which full soil cover was obtained, total accumulated biomass, growth duration, height development and N-accumulation were observed. Persian clover (*Trifolium resupinatum* L.) and subterranean clover (*T. subterraneum* L.) were the two most contrasting species in this study, particularly differing in the period in which full soil cover was obtained. Persian clover's faster soil cover could not be attributed to a single trait, but resulted from a number of intrinsic characteristics, like light extinction coefficient, light use efficiency and specific leaf area that together determine the relative growth rate. The study also demonstrated the importance of differences in relative starting position, caused by, for instance, seed size, seeding rate and fraction establishment, for the analysis of early growth characteristics. Alsike clover (*T. hybridum* L.), berseem clover (*T. alexandrinum* L) and crimson clover (*T. incarnatum* L.) developed slower than Persian clover, but all produced a higher amount of accumulated dry matter, due to a longer growing period. Clear differences in height and height development between species were observed. These differences were not associated with dry matter accumulation, as the tallest (red clover; 80 cm) and the shortest species (subterranean clover; 12 cm) produced similar amounts of dry matter. A strong positive correlation between early soil cover development and N-accumulation was observed. The large variability among clover species indicates that species selection is a very important aspect of the development of cropping systems that include clover as a cover crop.

Keywords: Clover; Undersown cover crop; RGR; Living mulch; Light interception; Soil cover; LUE; LAI; SLA

1. Introduction

The primary objective of weed management is to reduce the negative effects of weeds on crop production. Herbicides have proven to be a reliable and highly effective method to control weeds at relatively low cost. Consumers of the industrialized world however, increasingly demand food products that are safe, of high quality and have been produced with a minimum use of synthetic inputs. For that reason, weed management has to rely on other control measures. Achieving an adequate weed control without the use of herbicides is often reported to be difficult (Whitworth, 1995; Kropff and Walter, 2000). Mechanical weed control is often less effective, and moreover a heavy reliance on mechanical control is undesirable, because of damage to soil structure, increased risk of frost damage and the strong dependency on weather conditions. Removing weeds manually is often restrained by labour availability and is above all costly. Prevention of weed problems is another alternative, for which three mechanisms can be distinguished (Bastiaans et al., 2002). Firstly, the number of seeds that are present in the weed seed soil bank can be reduced. This can be achieved through increased seed mortality or a reduced seed production. Secondly, the fraction of seeds that develop into a weed seedling can be reduced through prevention of germination or emergence. Thirdly, growth and development of weed seedlings can be retarded to reduce the competitive ability of the weed relative to that of the crop, leading to a reduced negative effect on crop production.

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Undersown cover crops may potentially reduce weed infestation through each of the discerned mechanisms (Phatak, 1992). The effects of the cover crop are achieved by a rapid occupation of the open space between the rows of the main crop, which prevents germination of weed seeds and reduces the growth and development of weed seedlings. Germination of weed seeds may be inhibited by complete light interception (Phatak, 1992) by the cover crop or by secretion of allelo-chemicals (White et al., 1989; Overland, 1966). After establishment of weed seedlings, resource competition becomes the main weed suppressing mechanism of the cover crop (Teasdale, 1998).

The use of undersown cover crops for weed management is particularly relevant for crops that are not very competitive. Slow growing crops like leek and onion, with upright leaves, hardly form a closed canopy and are therefore not able to suppress weeds adequately (Baumann et al., 2001). Clover possesses good potential as a weed suppressor and apart from that has other advantages, like nitrogen fixation and the reduction of pests and diseases in a number of crops (Finch, 1993; McKinlay et al., 1995; Theunissen and Schelling, 1996). Ideally, the main crop and the cover crop should differ to a high degree in the way they explore resources, thus avoiding competition between both species to at least some extent (Vandermeer, 1989). The addition of clover as a cover crop, however, has often been reported to result in severe competition between the cover crop and the main crop (Bottenberg et al., 1997; Brandsaeter et al., 1998; Lotz et al., 1997; Weber et al., 1999). The subsequent yield losses are regarded as a serious constraint for using clover as an undersown cover crop (Liebman and Dyck, 1993; Brandsaeter et al., 1998; Hartwig and Ammon, 2002).

In conclusion, the beneficial effect of clover as a cover crop with respect to pest, disease and weed management can only be exploited if yield reduction resulting from competition can be reduced. Several attempts have been made to reduce the competitive strength of the undersown clover while maintaining its weed suppressing ability. Brandsaeter and Netland (1999) focused on temporal complementarity by separating periods of vigorous growth of the cover crop (subterranean clover) and the main crop, while Vrabel (1983) used chemical control of the cover crop to reduce yield losses. Brainard et al. (2004) evaluated different options, particularly, cover crop species, time of seeding, use of supplemental nitrogen and herbicide regulation. Ross et al. (2001) conducted mechanical control of the cover crop and combined this with a screening of different cover crops, including clover species. The screening revealed clear differences in the ability to suppress weeds among cover crops. Brandsaeter et al. (1998) demonstrated clear differences in competitive ability between different cultivars of subterranean and white clover and found that yield reduction of the main crop was positively correlated with biomass production of the clover species. To aid the selection of species for a particular crop and aid decisions about crop–weed management, Ross et al. (2001) remarked that a greater understanding of the growth characteristics of clover species is required. In this respect, several studies have indicated at the importance of (early) soil cover development (e.g. Brandsaeter and Netland, 1999; Brandsaeter et al., 1998; Baumann et al., 2000; Nelson et al., 1991). In crop–weed competition research early growth, particularly early leaf area development (e.g. Kropff et al., 1992), early height growth rate and final plant height (e.g. Bastiaans et al., 1997) have been identified as important characteristics determining the competitive ability of species. It is obvious that these traits are similarly important for strengthening the weed suppressive function of cover crops. Simultaneously, these characteristics determine the potential yield loss of the main crop resulting from competition with the introduced cover crop.

The current study focussed on a comparison of clover species. Main objective was to determine the variability in morphological and physiological traits that are considered relevant for inter-plant competition. If sufficient variation is available, species selection is likely to be one of the important means to optimize intercropping systems that contain clover for weed suppression. Competitive ability and the relation between the presented characteristics and competitive ability are covered in a second paper.

2. Materials and methods

In 2001, an experiment with eight clover species was conducted. Based on the results of this experiment three contrasting clover species were selected for further study in the 2002-experiment (Table 1).

2.1. 2001-Experiment

A screening experiment with eight clover species was laid out on a heavy clay soil, in Wageningen, the Netherlands. The site was fertilized with 300 kg ha^{-1} 12–10–18 NPK 2 weeks before sowing. The experimental design was a fully randomized complete block design in six replicates and treatments consisted of eight clover species. On May 7, the clovers were sown at a rate of 20 kg ha^{-1} in plots of 6 m × 7 m. Seeds were sown with a seed drill of which the pipes were positioned 30 cm above the soil surface to mimic broadcast sowing. After sowing, the soil was rolled with a Cambridge roller to compress the soil. Hand weeding of the clover plots was carried out at the end of June.

In each plot, the number of emerged clover plants was counted daily in two squares of 0.50 m × 0.50 m until no further increase in plant number was observed. Soil coverage was assessed weekly by estimating the soil cover in each of the 16 squares (0.125 m × 0.125 m) of a frame of 0.50 m × 0.50 m. Canopy height was determined weekly, at three positions per plot. Starting from 1 month after sowing, two squares of 0.50 m × 0.50 m were harvested weekly from each plot. The clover plants were cut just above soil level. A sub-sample was taken and used to determine the fraction leaf and stem. Leaf area was measured using a LI 3100 Area Meter (LI-COR, Lincoln, NE, USA). All samples were dried for 24 h at 70 °C and weighed subsequently. Leaf area index (LAI) was used to calculate the fraction light interception according to:

$$\frac{I}{I_0} = e^{(-k\,\mathrm{LAI})} \tag{2.1}$$

where I/I_0 is the fraction intercepted light, k the extinction coefficient (determined in a separate experiment; see below) and

Table 1
Clover species used in the experimental work of 2001 and 2002 (marked with an asterisk)

Clover species	Cultivar	Common name	1000-Grain weight	2001		2002	
				Seedlings	Ratio	Seedlings	Ratio
T. hybridum	Dawn	Alsike clover	0.83 f	177 bc	0.07 e		
T. alexandrinum	Alex	Berseem clover	3.17 b	256 b	0.41 b		
T. incarnatum	Contea	Crimson clover	2.94 c	235 bc	0.35 c		
*T. resipunatum**	Accdia	Persian clover	1.48 e	671 a	0.50 a	715 b	0.53 a
T. pratense	Violeta	Red clover	2.04 d	203 bc	0.21 d		
*T. subterraneum**	Mount Barker	Subterranean clover	6.28 a	115 c	0.36 bc	136 c	0.43 b
*T. repens**	Aran	White (c1) clover, large leaved	0.71 f	181 bc	0.07 e	873 a	0.31 c
T. repens	Riesling	White (c2) clover, medium leaved	0.78 f	170 bc	0.06 e		
SED			0.117	60.3†	0.028†	50.66†	0.018†

1000-Grain weight (g), density of established seedlings (seedlings m^{-2}) and ratio between seedlings and sown seeds of the clover species used in the field experiments of 2001 and 2002. Standard error of difference (SED) is presented for non-transformed data while the highest standard error of difference (SED_{max}) of the various pair wise comparisons is presented for transformed data. Different letters (a–f) within a column indicate significant differences at the 0.05 level; NS: not significant.
† SED maximum.

LAI is the leaf area index of the canopy. Daily values for light interception were obtained by fitting a logistic function through the calculated fraction light interception on the various sampling dates. Daily radiation interception (MJ m^{-2} day^{-1}) was calculated by multiplying the fraction light interception by the daily incoming photosynthetically active radiation as measured on a nearby weather station. Integration of the daily values resulted in the cumulative radiation interception (MJ m^{-2}) Simple linear regression analysis was carried out to investigate the relation between accumulated dry matter and the cumulative amount of intercepted light. The slope of the line represents light use efficiency (LUE; g MJ^{-1}).

The k values used for calculating the light interception of 2001 were assessed in an additional experiment in 2003. In this experiment, clover species were sown on May 7 in plots of 5 m × 3 m at a density of 20 kg ha^{-1}. The clover plots were kept weed free throughout the experiment. Light interception, using a SunScan Canopy Analysis System (Delta T Devices Ltd., Cambridge, UK) was measured in an area of 1 m^2, after which half of this area was harvested. A sub-sample was taken and used to determine the fraction leaf and stem. Leaf area of the sub-sample was assessed using a LI 3100 Area Meter. Samples were weighed after drying for 24 h at 70 °C. For the eight clover species this was done on average four times between June 4 and August 28.

2.2. 2002-Experiment

From the eight clover species that were evaluated in the 2001 field trial three contrasting clover species were selected for further evaluation (Table 1). Plots of 3 m wide and 5 m long were laid out on a sandy soil in Wageningen, the Netherlands. The experimental design was a split plot design in four replicates with N-level (0, 50 and 150 kg N ha^{-1}) as main factor and clover species as sub-factor. K and P fertilization was applied 1 month before sowing (100 kg ha^{-1} 60% K_2O and 200 kg 46% P_2O_5). Mechanical weed control was carried out 1 day prior to seed bed preparation. Inoculated (SelfStick Legume Inoculant; MicroBio Limited, Herts, UK) clover was sown on May 21 at a rate of 20 kg ha^{-1} using the same procedure as used in 2001. Hand weeding was carried out on June 13 and 14 in all plots and a second hand weeding was carried out on June 26.

Clover establishment, soil coverage and height were assessed using the same methodology as in 2001. Light interception measurements were done on June 19 (29 DAS), June 26 and 27 (36 and 37 DAS), July 19 and 20 (59 and 60 DAS) and August 2, 4, 5 and 7 (73, 75, 76 and 78 DAS). Two squares of 50 cm × 50 cm were harvested from the clover plots on July 1, July 15, August 12 and August 27 (41, 55, 83 and 98 DAS). The harvested material was treated in the same way as was done in 2001. At 41 and 83 DAS, the observations on shoot dry matter development were extended by taking eight soil cores of 30 cm deep with a diameter of 5 cm to assess root dry matter. The soil cores were cut in three parts of 10 cm each and pooled layer wise. Soil was washed out until clean roots remained. The roots were dried for 24 h at 70 °C. Abundance of root nodulation of the various clover species was assessed in the first week of August. A relative scale with five levels, ranging from very poor to very abundant was used. Additionally, activity of root nodules was investigated by slicing the nodules in half. Nodules with a red content were considered active while white nodules were considered in-active.

2.3. Statistical analysis

A Generalized Linear Model (GLM) with a log link function was used for analysing the number of established seedlings. The seedling density as a fraction of sown seeds was analysed using a GLM with a logit link function. Approximate values of the standard error of difference (SED) and least significant difference (LSD) ($p = 0.05$) were calculated. ANOVA was performed and LSD ($p = 0.05$) was calculated for the dry matter data of each harvest. For 2001, dry matter accumulation, soil cover and the fraction intercepted light were fitted to a logistic model,

$$y_t = \frac{c}{1 + e^{(-b(t-m))}} \tag{2.2}$$

where c is the upper asymptote, t the time in days after sowing (DAS), m the time at which y obtained 50% of c and b is the maximum relative growth rate. For 2002, only soil cover was fitted to the logistic model. For dry matter accumulation the 50% point (m) was estimated by linear interpolation of the two harvests nearest to the 50% point.

A weight factor (1/standerd error; S.E.) was included in the fitting procedure of the biomass data of 2001, to correct for heterogeneity of variance. Binomial distribution was assumed for soil cover data and normal distribution was assumed for the calculated light interception data. Pair wise comparisons were made between the estimated parameters of different species by calculating the t-statistic. Root dry matter and root dry matter as fraction of the total dry matter were analysed by performing ANOVA and calculating the LSD. All statistical procedures were carried out using the Genstat 7 statistical package (Payne, 2003).

3. Results

3.1. Establishment

In the 2001-experiment, at the first observation date at 5 days after sowing (DAS), plots with Persian clover already contained a considerable number of emerged plants, whereas in all other plots no emergence was observed. After 8 days no further increase in number of emerged plants was observed for Persian clover (Table 1). The other species reached their maximum number of emerged seedlings at about 11 DAS, except for red clover which obtained its maximum number at about 13 DAS. The fraction establishment varied considerably and ranged between 0.06 for white (c2) clover and 0.50 for Persian clover. In 2002, emergence of the selected species was more rapid, Persian clover reached maximum establishment at 6 DAS, white clover at 8 DAS and subterranean clover at 10 DAS. For Persian clover, the fraction establishment was almost identical to that in 2001, while the number of subterranean clover seedlings was slightly higher than in 2001. White (c1) clover had a much better establishment than in 2001, as the fraction established seedlings increased from 0.07 to 0.31.

The different fertilization rates in the 2002-experiment had no effect on emergence and establishment. Of the other traits only specific leaf area (SLA) at the first harvest (41 DAS) and shoot N-content were affected. For that reason only the average response of the various clover species at the three nitrogen levels was presented.

3.2. Dry matter accumulation

For 2001, the dry matter accumulation in time for each of the clover species could be adequately described by a logistic model. In Fig. 1 this is illustrated for Persian, subterranean and white (c1) clover, while the estimated parameters for all species are presented in Table 2. The estimated maximum shoot dry matter varied between 425 g m^{-2} (white (c2) clover) and 774 g m^{-2} (alsike clover).

The highest maximum growth rates (about 16 g m^{-2} day^{-1}) were obtained by Persian clover and alsike clover. Whereas Persian clover had the highest relative growth rate (RGR; 0.15 day^{-1}), alsike clover was among the species with the lowest RGR (0.08 day^{-1}). At the same time alsike clover had a much longer growing period than Persian clover and reached its maximum growth rate 30 days later than Persian clover. This resulted in a final accumulated dry matter (774 g m^{-2}) of nearly twice the amount produced by Persian clover (426 g m^{-2}). Red clover, crimson clover and berseem clover had maximum growth rates between 14 and 15 g m^{-2} day^{-1} and their final accumulated dry matter varied between 520 g m^{-2} (red clover) and 634 g m^{-2} (crimson clover). Subterranean clover and both white clover varieties had clearly the lowest maximum growth rates (about 12 g m^{-2} day^{-1}). Still those species produced nearly similar amounts of shoot dry matter as Persian clover. This is mainly because Persian clover had a relatively short growing period and obtained 50% of its total accumulated dry matter already at 54 DAS. Subterranean clover and the white clover species had a much longer growing period, reflected in a 50% point which was reached 17–22 days after Persian clover.

In 2002, when three clover species were selected for further analysis, final amounts of accumulated shoot dry matter of Persian, subterranean and white (c1) clover were not significantly different from each other and lower or equal to that obtained in 2001. Subterranean and white (c1) clover in particular reached the 50% point more rapidly than in 2001. For Persian clover the difference between both years was negligible. In 2002, root dry matter was assessed on 41 DAS and 83 DAS. Total root dry matter, the fraction root and the vertical root distribution in the upper 30 cm of the soil are presented in Table 3. Total root dry matter of white (c1) clover was significantly higher than the total root dry matter of Persian clover and subterranean clover, both

Table 2
Estimated parameter values obtained by fitting a logistic function to observed values for shoot dry matter of various clover species for 2001

Species	b	GR_{max}	m	c
2001				
Alsike clover	0.082 (0.009) b	15.90	84 (3) a	773.5 (46.3) a
Berseem clover	0.114 (0.012) ab	15.28	67 (2) c	535.1 (31.6) bc
Crimson clover	0.092 (0.009) b	14.63	76 (2) ab	633.7 (36.8) b
Persian clover	0.152 (0.016) a	16.12	54 (2) d	425.5 (26.1) d
Red clover	0.111 (0.013) ab	14.43	71 (2) bc	520.0 (33.0) cd
Subterranean clover	0.103 (0.013) b	11.55	71 (3) bc	448.5 (33.7) cd
White (c1) clover	0.100 (0.017) ab	11.70	76 (3) ab	469.7 (36.5) cd
White (c2) clover	0.113 (0.021) ab	12.04	74 (3) bc	424.9 (34.3) d
2002				
Persian clover			48	391.0
Subterranean clover			53	439.0
White (c1) clover			48	427.2
SED				NS

b: relative growth rate (RGR; day^{-1}); m: moment at which 50% of the maximum dry matter has been obtained expressed in days after sowing (DAS); c: maximum accumulated dry matter (DM; g m^{-2}). The maximum growth rate (GR_{max}; g day^{-1}) was derived from the estimated parameters. For 2002, m was derived by plotting 50% of the maximum obtained dry matter linearly between the first and the second dry matter measurement and c was the maximum dry matter obtained. Different letters (a–d) within a column indicate significant differences at the 0.05 level; values in parentheses denote S.E.; NS: not significant; RGR: relative growth rate; GR: growth rate.

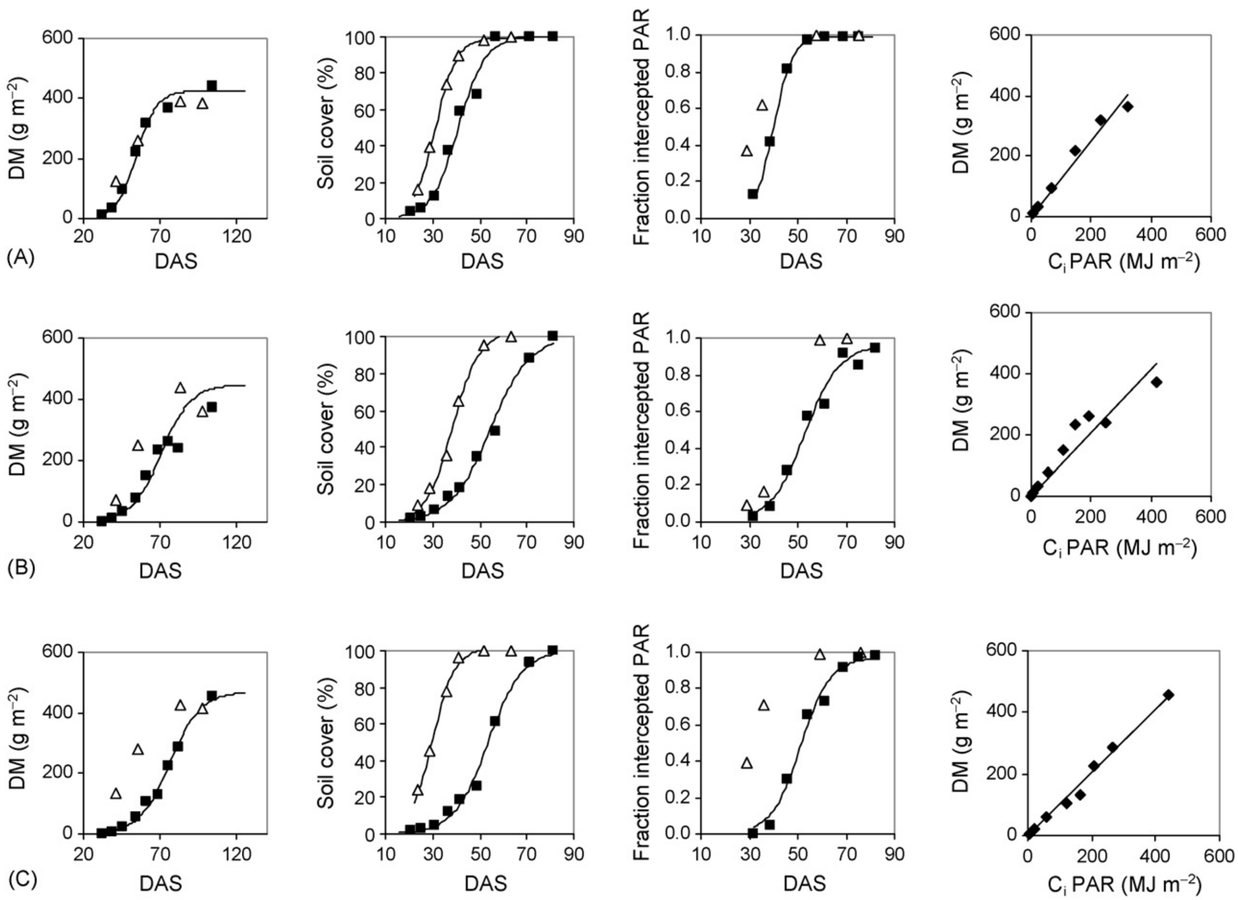

Fig. 1. Fitted and observed values for (from left to right) accumulated dry matter, soil cover, fraction intercepted photoactive radiation (PAR) and light use efficiency for Persian clover (row A), subterranean clover (row B) and white (c1) clover (row C) for 2001 (solid line) and 2002 (open triangle).

at 41 and 83 DAS. At 41 DAS, each species had invested nearly 20% of their total accumulated amount of dry matter into root growth, whereas at 83 DAS white (c1) clover had allocated a significantly higher fraction to the root (15%) than Persian (10%) and subterranean clover (9%).

At both dates small species differences in vertical root distribution were observed. At 41 DAS, white (c1) clover had a higher fraction (0.79) of its root material in the top soil layer (0–10 cm) than subterranean clover (0.68). Subterranean clover in turn had a higher fraction root dry matter in the lower zone. A similar trend was observed at 81 DAS, but then differences were not significant. The distribution of Persian clover held an intermediate position and did not differ significantly from either of the two species.

Table 3
Root dry matter (g m^{-2}), the fraction root dry matter (DM) of the total dry matter and the vertical root distribution (fraction) over the upper 30 cm of the soil at 41 and 83 DAS

Species	Root DM	Fraction root DM	Root distribution		
			0–10 cm	10–20 cm	20–30 cm
41 DAS					
Persian clover	23.9 b	0.18	0.75 ab	0.18	0.08 ab
Subterranean clover	15.3 c	0.18	0.68 b	0.18	0.13 a
White (c1) clover	31.4 a	0.19	0.79 a	0.15	0.06 b
SED	3.32	NS	0.040	NS	0.022
83 DAS					
Persian clover	41.1 b	0.10 b	0.71	0.17	0.12
Subterranean clover	46.8 b	0.09 b	0.69	0.19	0.13
White (c1) clover	75.6 a	0.15 a	0.75	0.16	0.08
SED	11.09	0.020	NS	NS	NS

Different letters (a–c) within a column indicate significant differences at the 0.05 level; NS: not significant; DAS: days after sowing.

Table 4
Leaf weight ratio (LWR; g leaf DM (g total above ground DM^{-1})) and specific leaf area (SLA; cm^2 (g leaf DM^{-1})) at three moments (DAS)

Species	LWR			SLA			$T_{LAI=3}$	LAI_{max}	$T_{LAI=max}$
	39 DAS	54 DAS	75 DAS	39 DAS	54 DAS	75 DAS			
2001									
Alsike clover	0.80 a	0.61 a	0.44 ab	201.0 cd	362.5 b	390.3 b	65	5.0	75
Berseem clover	0.57 c	0.36 c	0.30 c	292.2 a	422.7 a	347.5 d	68	3.7	75
Crimson clover	0.77 a	0.63 a	0.49 a	207.1 cd	339.3 bc	359.2 c	62	5.1	75
Persian clover	0.64 b	0.36 c	0.30 c	241.2 b	425.6 a	423.3 a	52	4.5	75
Red clover	0.75 a	0.60 a	0.41 b	222.4 bc	335.5 bc	337.9 cde	65	4.5	75
Subterranean clover	0.66 ab	0.47 b	0.33 c	172.7 e	287.8 c	260.9 f	79	3.5	82
White (c1) clover	0.76 a	0.63 a	0.45 ab	187.0 de	306.3 bc	312.5 e	71	4.4	82
White (c2) clover	0.78 a	0.61 a	0.44 ab	173.9 e	294.1 c	328.2 de	73	4.6	82
SED	0.026	0.028	0.026	12.77	28.22	14.47			
Species	LWR			SLA			$T_{LAI=3}$	LAI_{max}	$T_{LAI=max}$
	41 DAS	55 DAS	83 DAS	41 DAS	55 DAS	83 DAS			
2002									
Persian clover	0.50	0.27 c	0.20 c	507.2 a	494.7 a	370.6	40	3.6	55
Subterranean clover	0.57	0.31 b	0.26 b	350.0 b	343.4 b	377.0	62	4.9	98
White (c1) clover	0.53	0.36 a	0.32 a	480.4 a	507.5 a	395.1	37	5.4	83
SED	NS	0.017	0.019	19.16	20.26	NS			

The moment at which a leaf area index (LAI) of three was reached $T_{LAI=3}$ (DAS) and the maximum leaf area obtained (LAI_{max}) and the moment at which LAI_{max} was obtained $T_{LAI=max}$ (DAS) for various clover species for 2001 and 2002. Different letters (a–f) within a column indicate significant differences at the 0.05 level; DM: dry matter; DAS: days after sowing; NS: not significant.

3.3. Leaf area development, soil cover and light interception

In 2001, at 39 DAS, the fraction leaf dry matter ranged from 0.57 (berseem clover) to 0.80 (alsike clover) (Table 4). Also at the later harvests it was obvious that alsike clover invested a relatively large proportion of its shoot dry matter into the leaves. Other species that invested a high amount of shoot dry matter into their leaves were white (c1 and c2) clover, red clover and crimson clover. The low fraction leaf dry matter of berseem clover indicates that a large fraction of the above ground material was invested in the stem. The same was observed for Persian clover and subterranean clover. The specific leaf area (SLA; $cm^2\ g^{-1}$ leaf DM) of berseem and Persian clover were among the highest for each observation date. Alsike clover showed a clear increase in SLA over time, whereas the ranking of the other species remained fairly constant. Both white clover varieties and subterranean clover had the thickest leaves throughout the growing period. In 2002, the fraction leaf dry matter was generally lower than in 2001. As in 2001, white clover invested a higher fraction of its dry matter in leaves than subterranean clover, whereas Persian clover invested the smallest fraction. Subterranean clover produced thicker leaves than Persian and white (c1) clover, except for the last harvest at 83 DAS, when this difference had disappeared.

In 2001, Persian clover had a more rapid increase in LAI than the other clover species (Table 4). It reached an LAI of 3 at least 10 days before the other clover species. Persian clover's rapid increase in LAI corresponds to its rapid increase in shoot dry matter, and was realized despite its relatively low LWR. Berseem clover reached a maximum LAI of 3.7, which was lower than the LAI of the other three clovers that accumulated high amounts of shoot dry matter (alsike, 5.0; crimson, 5.1; red clover, 4.5). This was due to differences in allocation pattern, with berseem clover investing a relatively high fraction of its shoot dry matter into stem material. Subterranean clover and white clover (both varieties) showed a slow initial leaf area development, but continued to increase in LAI after 81 DAS, when the LAI of all other clovers started to decline. Still, subterranean clover only reached a maximum LAI of 3.7.

In 2002, Persian clover even had a faster initial leaf area development than in 2001, though its maximum LAI remained lower. White (c1) clover and subterranean clover also had a faster development than in 2001. White (c1) clover even reached an LAI of 3 before Persian clover. Both white (c1) clover and subterranean clover reached a higher maximum LAI than in 2001.

Observations on soil cover were conducted between 21 and 87 DAS. For all species full soil cover was reached and the development of soil cover over time could be accurately described by a logistic function. Persian clover reached full soil cover at 57 DAS, well before the other clover species (Table 5). This rapid soil cover development was most clearly expressed in the early moment (41 DAS) at which 50% soil cover was obtained. This was between 9 and 14 days earlier than for the other clover species. No significant differences between red, crimson, alsike (52, 51 and 52) and white (c1 and c2) and subterranean clover (54, 54 and 55) were obtained for the time to achieve 50% soil cover. Berseem clover however, reached this point significantly faster than subterranean and both white clover varieties. In 2002, soil cover measurements were conducted between 24 and 63 DAS, and again the development in soil cover could be well described by a logistic function. Persian, white (c1) and sub-

Table 5
Estimated parameter values obtained by fitting a logistic function to observed values of soil cover and light interception (LI)

Species	*b* (soil cover)	*m* (soil cover)	*b* (LI)	*m* (LI)	*k* value
2001					
Alsike clover	0.15 (0.012)	52 (1.0) ac	0.22 (0.014) ab	49 (0.8) bc	0.83
Berseem clover	0.15 (0.007)	50 (0.5) bc	0.22 (0.034) ab	45 (0.3) d	0.97
Crimson clover	0.13 (0.016)	51 (1.5) ac	0.17 (0.031) b	46 (0.3) d	0.86
Persian clover	0.18 (0.024)*	41 (1.1) d	0.25 (0.008) a	40 (0.1) e	1.04
Red clover	0.13 (0.012)	52 (1.2) ac	0.21 (0.018) ab	48 (0.5) c	0.79
Subterranean clover	0.12 (0.011)*	54 (1.3) a	0.14 (0.027) b	56 (1.7) a	0.80
White (c1) clover	0.14 (0.011)	54 (1.0) a	0.17 (0.031) b	51 (1.3) ab	0.94
White (c2) clover	0.14 (0.014)	55 (1.3) a	0.15 (0.024) b	53 (1.3) a	0.90
SED	NS				NS
2002					
Persian clover	0.22 (0.006)	31 (0.2) a			
Subterranean clover	0.18 (0.019)	39 (0.7) b			
White (c1) clover	0.21 (0.018)	30 (0.4) a			
SED	NS				

b: relative growth rate (RGR; day^{-1}); *m*: moment at which 50% of the maximum was reached (DAS) for various clover species for 2001 (soil cover and LI) and 2002 (LI). Estimated extinction coefficient (*k* value) for various clover species based on field observations collected during the 2003 growing season. Different letters (a–e) indicate significant, within column, per season, differences at 0.05 level; values in parentheses denote S.E.; NS: not significant.
* Significantly different at 0.10 level.

terranean clover reached full soil cover at or before 63 DAS (Fig. 1) which was faster than in 2002. Subterranean clover and white (c1) clover in particular had a much faster increase in soil cover in 2002 than in 2001. Soil cover development of white (c1) clover was almost identical to that of Persian clover, while that of subterranean clover lagged behind.

Light interception for the various clover species in 2001 was based on observed LAI data and the experimentally determined light extinction coefficients (*k*). Values of *k* ranged from about 0.8 (red, subterranean and alsike clover) to around 1.0 (Persian clover), but differences were not significant (Table 6). The logistic model gave an accurate description of the light interception data ($R^2 > 0.97$). Light interception of Persian clover increased more rapidly than that of the other species, whereas the slowest increase in light interception was obtained for white clover and subterranean clover (Table 6). The light interception measurements of 2002 confirmed the observations on soil cover. Light interception of Persian clover and white (c1) clover developed as fast as light interception of Persian clover in 2001. Light interception of subterranean clover developed faster than in 2001, but still lagged behind white (c1) and Persian clover.

Fig. 2 illustrates that soil cover and light interception were highly correlated. It is clear that with an increase in soil cover more light was captured. For some species, like subterranean clover, the rate of increase in light interception was nearly proportional to the rate of increase in soil cover. For other species, like berseem clover, light interception developed slightly faster than soil cover. It is clear that species that grew tall (e.g. berseem clover; see below) showed a relative faster increase in light interception compared to soil cover than species that remained low (e.g. subterranean clover). The relation between light interception and soil cover for the two white clover species was similar to that of subterranean clover. The remaining species all showed a similar relationship as was found for berseem clover.

3.4. Light use efficiency

Data for 2001 were used to determine the light use efficiency. For this purpose, the amount of accumulated dry matter during the exponential and the linear growth phase was related to cumulative intercepted PAR by simple linear regression. The slope of the fitted line represents LUE. For Persian clover only observations up to 75 DAS were used, as senescence for this species

Table 6
Canopy height (cm) at four moments for various clover species in 2001 and 2002

Species	Canopy height			
	38 DAS	46 DAS	54 DAS	84 DAS
2001				
Alsike clover	1.9 d	5.8 d	12.1 d	37.3 d
Berseem clover	14.6 a	25.6 a	51.1 a	49.5 b
Crimson clover	4.1 c	6.3 a	9.3 e	47.6 bc
Persian clover	9.6 b	13.8 b	31.0 b	46.5 c
Red clover	5.5 c	9.7 c	17.2 c	80.0 a
Subterranean clover	0.9 e	1.0 e	3.6 f	11.6 g
White (c1) clover	1.9 d	4.9 d	10.4 e	23.7 f
White (c2) clover	2.1 d	4.7 d	9.2 e	27.7 e
SED	0.86	1.49	0.60	1.38
Species	**Canopy height**			
	41 DAS	52 DAS	61 DAS	79 DAS
2002				
Persian clover	25.4 a	37.9 a	45.1 a	42.9 a
Subterranean clover	10.0 c	18.7 c	25.6 c	21.4 c
White (c1) clover	20.7 b	24.8 b	29.5 b	31.2 b
SED	1.42	1.46	1.16	1.41

Different letters (a–g) within a column indicate significant differences at the 0.05 level; DAS: days after sowing.

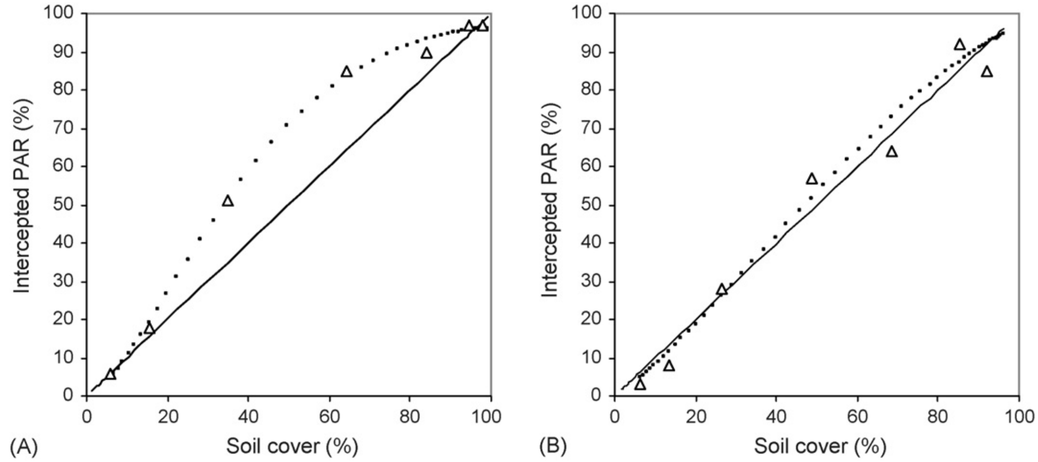

Fig. 2. The relation between the percentage of intercepted PAR and the percentage soil cover for berseem clover (A) and subterranean clover (B) for 2001.

started soon after this date. For all other species observations until 104 DAS were included. A strong linear relation was found for all species and examples for three clover species are given in Fig. 1. LUE varied from 1.03 g DM MJ^{-1} for subterranean clover till 1.25 g DM MJ^{-1} for Persian clover (Table 5).

3.5. Height development

In Table 6, height of the various clover species is presented for four different dates. In 2001, berseem clover was by far the fastest growing species in height as it reached its maximum height (51 cm) well before any of the other clover species. This observation corresponds well with the observation that berseem invested a large fraction of shoot dry matter into stem material. However, a heavy shower directly after the measurement on 54 DAS reduced its height to 31 cm. At 84 DAS red clover, which reached a maximum of 80 cm, was the tallest species. Observations on height were carried out until this date, as strong showers directly after the measurement on 84 DAS considerably reduced the height of all species except that of subterranean clover and both white clover varieties. Next to berseem clover, Persian clover had a rapid height development, whereas subterranean clover and both white clover cultivars had the slowest development in height. Both Persian clover and subterranean clover invested a relative high fraction of their shoot dry matter into the stem. For Persian clover this resulted in a rapid height development while for subterranean clover an extensive lateral development was observed. Bulk densities determined at 54 DAS confirmed these findings and were highest for subterranean clover (2.60×10^{-3} g cm^{-3}) and lowest for berseem clover (0.22×10^{-3} g cm^{-3}). In 2002, at around 60 DAS, subterranean clover and white (c1) clover were about 20 cm taller than in the 2001 growing season. Persian clover also grew taller more rapidly in 2002 but did not obtain a larger maximum height.

3.6. Nitrogen accumulation

In 2001 (75 DAS) and in 2002 (55 DAS) clover samples were analysed for total nitrogen (N) content of the shoot (Table 7). In 2001, alsike clover and Persian clover accumulated the highest amounts of N (10.8 and 12.0 g m^{-2}, respectively). These species were also among the clover species with the highest N-content (3.73 and 3.36%). Berseem clover accumulated nearly as much N as Persian and alsike clover but had a much lower N-content (2.52%). Crimson clover and subterranean clover also had a relatively low N-content (2.59 and 2.26%). Subterranean clover accumulated the lowest amount of N (5.53 g m^{-2}).

In 2002, no significant differences between species were observed for both the amount of accumulated N and N-content. N-fertilization had a significant effect on the N-content, resulting in a significantly higher N-content at the highest fertilization rate.

Table 7
Clover dry matter (DM) (g m^{-2}), N-content (%) and the amount of total accumulated N (g N m^{-2}) at 75 DAS (2001) and 55 DAS (2002) in dependency of species and N-fertilization rate

Species	DM	N-content	N-total
2001			
Alsike clover	293.0 b	3.73 a	10.77 a
Berseem clover	359.2 a	2.52 b	9.18 ab
Crimson clover	291.2 b	2.59 b	7.59 bc
Persian clover	354.4 a	3.36 a	12.00 a
Red clover	286.0 b	3.37 a	7.59 bc
Subterranean clover	254.6 b	2.26 b	5.53 c
White clover (c1)	225.8 b	3.45 a	7.83 bc
White clover (c2)	222.4 b	3.49 a	7.78 bc
SED	48.44	0.248	1.46
2002			
Persian clover	260.1	2.87	7.46
Subterranean clover	250.4	2.66	6.66
White clover (c1)	282.8	2.86	7.78
SED	NS	NS	NS
N1	301.9	2.56 b	7.60
N2	237.7	2.71 b	6.36
N3	253.7	3.13 a	7.94
SED	NS	0.189	NS

Different letters (a–c) within a column indicate significant differences at the 0.05 level; NS: not significant.

Table 8
Correlation coefficients (r) between number of traits determined for eight clover species/cultivars in 2001

	$b_{\text{soil cover}}$	b_{LI}	b_{DM}	$T_{\text{LAI=3}}$	$\text{DM}_{\text{61 DAS}}$	DM_{max}	$\text{Height}_{\text{max}}$	N-total
$b_{\text{soil cover}}$	1	0.79**	0.67	−0.75*	0.72*	0.06	0.15	0.94***
b_{LI}		1	0.46	−0.81**	0.72*	0.25	0.61	0.87***
b_{DM}			1	−0.50	0.75*	−0.69	0.21	0.43
$T_{\text{LAI=3}}$				1	−0.78*	−0.18	−0.58	−0.80**
$\text{DM}_{\text{61 DAS}}$					1	−0.15	0.32	0.63
DM_{max}						1	0.21	0.27
$\text{Height}_{\text{max}}$							1	0.28
N-total								1

RGR for soil cover development ($b_{\text{soil cover}}$), light interception (b_{LI}) and dry matter production (b_{DM}), moment at which a leaf area index of 3 was reached ($T_{\text{LAI=3}}$), the obtained dry matter at 61 days after sowing ($\text{DM}_{\text{61 DAS}}$), the estimated maximum obtained dry matter (DM_{max}), the maximum canopy height ($\text{Height}_{\text{max}}$) and the total amount of accumulated nitrogen (N-total).

* $p < 0.10$; two-tailed.

** $p < 0.05$; two-tailed.

*** $p < 0.01$; two-tailed.

3.7. Correlation analysis

For a number of relevant traits a correlation study was conducted (Table 8). As expected, RGR's of soil cover and light interception, were strongly positively correlated ($p < 0.05$). The RGR of shoot dry matter accumulation was not significantly correlated with these two measures. This might be due to differences in allocation pattern (Table 5). Two other measures that represent early growth (the moment at which a leaf area index of 3 was reached ($T_{\text{LAI=3}}$) and the obtained dry matter at 61 days after sowing ($\text{DM}_{\text{61 DAS}}$) were closely correlated with the RGR's of soil cover and light interception. No significant correlation between height and any of the other traits was detected. Total nitrogen accumulation correlated strongly and positively ($p < 0.01$) with the RGR's of soil cover, light interception and $T_{\text{LAI=3}}$. This suggests that nitrogen accumulation benefits from a fast development, resulting in pre-emption of below-ground resources.

4. Discussion

In this study, a comparison of various clover species was made. A number of growth characteristics was determined with the aim to investigate the variability among species. Particular attention was given to those characteristics that are expected to affect the suitability of clover as an undersown cover crop for weed suppression in full field vegetable production. The variability among species determines the importance and opportunities of species selection as a component in the design of a suitable weed management system. A prerequisite for the selected species of this study was their commercial availability and adaptation to the temperate climate of Western Europe. In 2001, seven different clover species were selected to obtain a wide range of characteristics. Also within clover species clear differences in growth characteristics do exist (e.g. Holland and Brummer, 1999; Brandsaeter et al., 1998). But as the aim was to obtain a wide range of characteristics the emphasis was put on a comparison between species, and only for white clover two cultivars, differing in leaf size (large leaved; Aran, medium leaved; Riesling) were selected. It should thus be realized that the presented results are typical for the selected cultivar within a species. In 2002, three out of the eight clovers were selected for further evaluation (Persian clover, white clover (Aran) and subterranean clover). The three selected clover species were differing strongly in characteristics such as early growth, soil cover and height development that are relevant for competitive ability.

Weed suppression benefits from a rapid soil cover, as this reduces the germination and establishment of weeds as well as the relative competitive ability of established weed seedlings (Ross and Lembi, 1985). Differences in soil cover development do not only depend on species differences in morphology and physiology. The relative starting position, determined by, for instance, seed size, seeding rate and date of emergence, is another major factor in this respect. For the species selected in this experiment seed size differed with nearly a factor 10. To account for these differences in seed size, all clover species were sown at a fixed seeding rate of 20 kg germinable seeds ha^{-1}. A germination test in Petri-dishes revealed that for all species the percentage germination exceeded 97%. Despite the results of this test, a nearly eight-fold difference in fraction established seedlings was observed between Persian clover (0.50) and the small-seeded clover species (white and alsike clover; 0.06–0.07). As the relative growth rate for soil cover of the small-seeded species (0.14–0.15 day^{-1}) corresponds to a doubling time of 4.6–4.9 (=ln(2)/RGR) days, this lower fraction establishment corresponded to a delay of about 2 weeks. These figures illustrate that comparisons between species in initial development should consider establishment, or should focus on traits, like RGR, that are independent of establishment. At the same time, the results of 2001 suggest that small-seeded species are more sensitive to conditions that might cause a poor establishment. This was confirmed by comparing the results of 2001 and 2002. Whereas differences in establishment between years were very small for both Persian clover and subterranean clover, a remarkable improvement in establishment was observed for white (c1) clover. Not only did seedlings emerge about 3 days earlier, also the fraction of established seeds was considerably higher in 2002 (31% versus 7%). Most notable differences between both years were soil type (clay versus sand), the accumulated amount of precipitation in the 2 weeks around sowing

(3 mm in 2001 and 18.2 mm in 2002) and a heavy shower at 7 DAS in 2001 (25.7 mm), which may have washed seeds away. As only white clover had a higher fraction of established seedlings, it suggests that for establishment this species, and perhaps more in general small-seeded species, are more sensitive to environmental conditions.

Persian clover had the fastest soil cover development of all species. To some extent this was due to its good starting position. Persian clover emerged 2–5 days before the other species and also had the highest fraction establishment. Further analysis however learned that this species also had the highest intrinsic growth rate. This was not only observed for soil cover ($p < 0.10$), but also for light interception and dry mater accumulation. The RGR reflects the increase of characteristics like soil cover and dry matter accumulation during early development, when growth is still exponential. In this period a strong positive feedback exists between radiation interception, crop growth and leaf area formation resulting in exponential growth (Blackman, 1919). The relative growth rate of a plant species is thus affected by its light capturing ability, by the efficiency by which it converts light into biomass and by the fraction of newly produced biomass which is invested in leaves. For the first two characteristics, the light extinction coefficient (k) and the light use efficiency, a wide range of values was obtained, though no significant differences between species were observed. Values for k ranged from 0.79 to 1.04, whereas LUE ranged between 1.03 and 1.25 g DM MJ^{-1}, values that correspond well to values reported for two white clover cultivars (Nassiri, 1998; 1.02 g DM MJ^{-1} for Alice and 0.96 g DM MJ^{-1} for Gwenda). Persian clover was characterized by high values for both traits. For the third characteristic, leaf area ratio (LAR = LWR × SLA), a moderate to high value was obtained. Values for SLA were always relatively high for Persian clover, but LWR was relatively low right from the start and declined faster than for most other species. This observation might be related to the rapid phenological development of Persian clover, which was expressed by for example early flowering, as plants often show a reduced LWR when ageing (Woolhous, 1967). Compared to Persian clover, subterranean clover was the only species that was characterized by a significantly lower RGR for soil cover ($p < 0.10$), dry matter accumulation and light interception. The low RGR's for subterranean clover are not surprising, as for all characteristics that together constitute the RGR (k, LUE, LWR and SLA) the value of subterranean clover was always among the lowest of all species. Of the two white clover cultivars, cultivar 'c1' (Aran) was used in both seasons. In 2001, white (c1) clover developed relatively slow for soil cover, light interception and dry matter accumulation, whereas in 2002 it developed as rapid as Persian clover. This difference could be explained by its much better starting position caused by a much higher fraction emergence, resulting in a nearly five times higher number of emerged seedlings. Furthermore, also its RGR was considerably higher than in 2001. This last observation was true for all three species and might be related to the higher average air temperature in the first month after emergence (14.2 °C for 2001 and 16.0 °C for 2002). In this study, white clover showed to be a more rapid developing species than subterranean clover which contradicts statements of Frame et al. (1998), who described the vigour of white clover seedlings as slow growing during early establishment, whereas the vigour of subterranean clover was described as moderate to high. Brandsaeter et al. (1998) concluded, based on experiments with undersown white and subterranean clover, that white clover had a slower soil cover development than subterranean clover. The sowing density of subterranean clover was, however, much higher than that of white clover, resulting in a different starting position. No information on establishment was provided, while our findings clearly show the importance of seedling density.

Clear differences were obtained in maximum amount of accumulated biomass. Alsike and crimson clover produced the highest amount of biomass. Biomass production of Persian clover, being the fastest developing species, was among the lowest, mainly due to its relatively short growth duration. For weed competition and weed suppression, earliness has been reported an important characteristic (de Haan et al., 1994). Particularly for competition for light, which is asymmetric (Weiner, 1986), obtaining a good starting position seems highly relevant. From that perspective the RGR seems to be a more important characteristic than the maximum accumulated amount of biomass.

Apart from soil cover development, height is an important characteristic, determining competition for light (e.g. Berkowitz, 1988). This effect was quantified by Kropff and van Laar (1993) in a simulation study. For the species represented in this study, no clear relation between total dry matter accumulation and maximum height was observed (Table 8). Alsike clover, being the species with the highest amount of accumulated dry matter, only reached a maximum height of nearly 40 cm, resulting in an intermediate position with respect to height. Furthermore, red clover, being the tallest species, and subterranean clover, being the shortest species, accumulated similar amounts of dry matter. Berseem clover also took a special position, as it was the species with the fastest height development during early growth stages. This observation was in line with the allocation pattern of berseem clover, which clearly invested a higher fraction of its shoot dry matter into stem material.

The overall competitive ability of a plant species does not only depend on its ability to compete for light but also on its ability to compete for water and nutrients (Tilman, 1988) of which nitrogen is of particular importance for plant growth. Obviously, the nitrogen accumulation of clover is realized by both N_2 fixation from the air and by uptake of nitrate from the soil. It is therefore difficult to attribute a low or high amount of accumulated nitrogen solely to a better or poorer below-ground competitive ability. That these two systems for nitrogen accumulation are present at the same time in clover may very well explain why the different amounts of nitrogen fertilization in 2002 did not affect the total amount of accumulated nitrogen for any of the clover species. Griffith et al. (2000) observed that at higher levels of available mineral soil nitrogen, the nitrogen fixation of white clover decreased, in other words, the available mineral nitrogen substitutes the nitrogen otherwise captured from the air. One other reason why the nitrogen fertilization may have had little effect on nitrogen uptake of clover, is because all nitrogen was applied 1 day after sowing well before the nitrogen demand of the growing plants was at its maximum. As the experiment was conducted on sandy soil and a number of heavy rain showers occurred during the first weeks after sowing, leaching of nitrogen may have taken place, resulting in much smaller differences in available soil mineral nitrogen than was intended. Even though fertilization did not result in differences in accumulated nitrogen, increases in shoot N-content and SLA were observed. An increased specific leaf area following higher N-fertilization is more often observed (e.g. green cabbage by Li et al., 1999).

In 2001, clear differences in N-accumulation between species were observed. The two species which had accumulated most nitrogen at 75 DAS, Persian clover and alsike clover, were characterized by a very distinct growth pattern. Persian clover had a short growth period, combined with a rapid initial growth, whereas alsike clover combined a long growth period with a slow initial growth. This implies that, at least in pure stand, a fast initial development is not a prerequisite for the accumulation of a high amount of nitrogen. Still the correlation analysis revealed a strong positive association between total N-accumulation and the RGR's of soil cover, light interception and the moment at which a LAI of 3 was reached. This is not surprising, as all other clover species, except for berseem clover, accumulated a significantly lower amount of nitrogen and were characterized by a relatively slow initial development. For subterranean and crimson clover the low amount of accumulated nitrogen was combined with a low N-content, indicating that for those species N-uptake might have been a growth limiting factor.

Aim of this study was to evaluate growth characteristics of a range of clover species. Specific attention was given to a number of traits like relative growth rate, total accumulated biomass, height development and N-accumulation that are expected to affect the suitability of clover as an undersown cover crop for weed suppression in full field vegetable production. The results showed that for most of these characteristics clear differences between species were present. Moreover, a correlation analysis revealed that hardly any correlations were present between the groups of traits that represent various aspects of competitive ability, like earliness, final amount of accumulated dry matter, height development and N-accumulation. As the various group of traits are not intertwined, competition experiments conducted with this group of selected species offers good opportunities to identify which traits are specifically responsible for differences in competitiveness. Results of such experiments will be discussed in a separate paper (den Hollander et al., 2007).

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