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Seedling-selection effects on morphological traits of mature plants in red clover

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Abstract Knowledge of the correlation between juvenile- and mature-plant traits is critical in determining the opportunities for early stage selection. The effects of early stage selection on mature-plant performance have rarely been quantified. This study was conducted to identify seedling traints in red clover (*Trifolium pratense* L.) that correlate to mature-plant traits and to evaluate the effect of seedling selection on forage yields and other mature-plant traits. The results showed that relationships between most seedling- and mature-plant traits were weak (r ranged from −0.170 to 0.239). Nevertheless, selecting the top 10% seedlings for petiole length, days from emergence to full expansion of the 4th leaf (D4LE), or leaves per seedling, produced a mature-plant population with higher individual plant dry weight (IPDW1) and higher annual yield in 1993 (Y93). Selection for leaves per seedling increased IPDW1 by 23.2%. Selection for petiole length and the smallest D4LE increased Y93 by 15.7% and 13.8%, respectively. Furthermore, substantial expected genetic gains were obtained for IPDW1 and Y93 when selecting for some seedling traits. We conclude that plants and families with low potential yield can be eliminated at the seedling stage in red clover. This will allow breeders to increase the number of superior plants to be field tested or to conduct a more rigorous evaluation of the selected plants. Among the five selection schemes tested for direct selection of mature-plant traits, mass selection produced the largest genetic gain.

Key words Correlation · Seedling selection · Red clover · Expected response to selection

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Introduction

Indirect selection, such as selection at the seedling stage for mature-plant traits, is important in plant breeding when the primary trait is difficult to measure or it is expensive to collect the data (Gallais 1983; Magnussen 1991). Selection for mature-plant traits of forage crops at a juvenile stage would be useful for forage breeders as a means to identify less-productive plants. A preliminary selection with low intensity may reduce the cost of a selection program by eliminating 'poor' plants or families with low potential yield, thus allowing the inclusion of more material with high yield potential or a more rigorous field evaluation of the superior plants.

Several seedling traits have been reported to be associated with mature-plant performance in some species. Bouton (1982) reported that alfalfa (*Medicago sativa* L.) seedling top weight and a visual size rating were positively correlated with the subsequent yield of spaced plants in the field. Simons (1989) determined that selecting the top 10% seedlings for either seedling dry weight or minimum days for expansion of the first trifoliolate leaf in alfalfa increased forage yields by 41% and 31%, respectively. These results were obtained despite the low correlations betweeen measured seedling traits and mature-plant yields. In common vetch (*Vicia sativa* L.), seedling traits were correlated with mature-plant biomass and reproductive performance (Qiu and Mosjidis 1993). The taproot-leaf weight ratio in 21-day-old sugar beet (*Beta vulgaris* L.) seedlings was correlated with photosynthate partitioning, thus affecting the economic yield. The responses observed in two cycles of selection indicated that the taproot-leaf weight ratio was genetically controlled (Snyder and Carlson 1978).

Selecting healthy, stout seedlings for subsequent crop production is a common practice in agriculture. However, previous reports showed that correlations between seedling traits and mature-plant traits were generally small, and the number of seedling traits identified to be associated with mature-plant performance were few

(Bouton 1982; Simons 1990; Qiu and Mosjidis 1993). Furthermore, the genetic effects of selecting seedling traits on mature-plant traits in most cases have not been quantified. Therefore, the objectives of our research in red clover were (1) to determine the relationships of seedling traits and mature-plant traits and (2) to evaluate the effect of seedling selection on forage yield and other mature-plant traits.

Materials and methods

A mixture of three red clovers 'Redland', 'Cherokee' and 'Renegade', all of them adapted to Alabama, were used to establish the base population in 1991–1992. Open-pollinated seeds of 80 individual plants visually selected for vigor and seed production were harvested. The resulting half-sib (HS) progenies were planted in the greenhouse at Auburn University on September 12, 1992, using multi-celled flats (Speedling Inc., Sun City, Fla.)[1] containing ProMix (Premier Brands Inc., Red Hill, Pa.)[1]. Each cell was overplanted and thinned randomly to one seedling per cell after emergence. A randomized complete block design with four replications was used. Each 'plot' consisted of 12 seedlings of each HS family.

Traits recorded on individual 5-week-old seedlings included leaves per seedling, length and width of the central leaflet in the largest leaf, length of the longest petiole (which was equivalent to height because seedlings were at the rosette stage), visual rating of seedling vigor (with a 1 to 9 scale where 1 = weak and 9 = vigorous), days from emergence to full expansion of the second (D2LE) and the fourth (D4LE) trifoliolate leaves, days from the date that the second and fourth trifoliolate leaves appeared until their full expansion. Furthermore, the average rate of leaf production of the first four leaves (RLP), RLP = 4/D4LE, and the leaf expansion rate of the second (R2LE) and the fourth (R4LE) leaf, R2LE or R4LE = $1/d$ (d = days from the date that leaf appeared until its full expansion), were calculated.

Seedlings were transplanted to the field at Tallassee, Alabama, in 1992, on a Hiwassee sandy loam soil (clayey, kaolinitic, thermic, typic Rhodudults). Twelve HS plants were 0.5 m spaced, transplanted in single-row plots 1.0 m apart, 5.5 m long. Forage yield was measured twice in 1993 and once in 1994. The experimental design was a randomized complete block with four replications. Data collected on an individual plant basis at harvest time in 1993 and in 1994 were: canopy height (CH cm); visual rating of plant vigor (VIG) using the same score as for seedling vigor; maturity score (MAT) in a 1 to 7 scale, where 1 = vegetative, without elongated stems (rosette stage); 2 = vegetative, with elongated stems (stem length > 10 cm); 3 = early bud, with inflorescence visible but partially wrapped up by the stipulses; 4 = mid bud, with inflorescence out of the stipules but no color in the flowers; 5 = late bud, with some flowers showing pinkish color; 6 = full flower, the flowers in the first head being at or just past anthesis; 7 = mature flower, the flowers in the first inflorescence having dry brownish petals; and individual plant dry weight (IPDW).

Pearson correlation coefficients were calculated among all the variables recorded. About 3800 individual plants were used to calculate correlation coefficients among the seedling traits and CH, VIG and MAT. Individual plant dry weight was measured in about 1900 plants in 1993. In 1994, mature-plant traits were measured in about 400 surviving plants (red clover plants live 1 to 2 years in Tallassee, Alabama). To evaluate the effect of selecting the top 10% for each seedling trait on the forage yield and mature-plant traits, the mean of whole population for each mature-plant trait was determined and compared with the mean of the selected plants using a t-test (SAS Institute 1988).

[1] Names of products are included for the benefit of the reader and do not imply endorsement or preferential treatment by the Alabama Agricultural Experiment Station, Abuburn University

Table 1 Analysis of variance of half-sib families in a randomized complete block design on an individual plant basis

Source of variation	*df*	MS	EMS
Replications	$(r-1)$		
Families	$(f-1)$	MS_F	$\sigma_W^2 + n\sigma_E^2 + rn\sigma_F^2$
Error	$(r-1)(f-1)$	MS_E	$\sigma_W^2 + n\sigma_E^2$
Within plots	$rf(n-1)$	MS_W	σ_W^2

Field data from individual plants measured in 1993 were subjected to analyses of variances (Table 1) using the model:

$$X_{ijk} = \mu + B_i + HS_j + B.HS_{ij} + E_{ijk}$$

where $i = 1, \ldots, r$, $j = 1, \ldots, f$, $k = 1, \ldots, n$; μ is the grand mean, B_i is the ith block effect, HS_j is the jth HS family effect, $B.HS_{ij}$ is block-family interaction, and E_{ijk} is the variation among n individual plants within plots.

Based on the model above, two types of heritability can be calculated: heritability on an individual plant basis (H1), $H1 = \sigma_A^2/\sigma_P^2 = 4\sigma_F^2/(\sigma_F^2 + \sigma_E^2 + \sigma_W^2)$, and heritability on a family mean basis (H2), $H2 = \sigma_A^2/\sigma_P^2 = \sigma_F^2/(\sigma_F^2 + \sigma_E^2/r + \sigma_W^2/rn)$ (Nguyen and Sleper 1983). The expected response to selection is given by $R = kh^2\delta = h^2S$, where k is the selection intensity, h^2 the heritability value, δ the square root of phenotypic variance, S the mean phenotypic value of selected plants, expressed as a deviation from the population mean (Falconer 1981). Three types of selection can be made based on the model described above: mass selection, using the heritability H1; family selectionl using the heritability H2; and combined selection, that is, family selection $k_1\sigma_F^2/(\sigma_F^2 + \sigma_E^2/r + \sigma_W^2/rn)^{1/2}$ together with $k_2 3\sigma_F^2/(\sigma_E^2 + \sigma_W^2)^{1/2}$ as within-family selection (Nguyen and Sleper 1983).

Five combinations of selection intensity of among and within families giving rise to the same final selection intensity (10%) were compared. They were: (1) 10% among- (k = 1.755) and 100% within-family selection; (2) 80% among- (k = 0.351) and 12.5% within-family (k = 1.647) selection; (3) 31.6% among- and 31.6% within-family (k = 1.125) selection; (4) 12.5% among-and 80% within-family selection; and (5) 100% among and 10% free selection (mass selection).

Results and discussion

Correlation coefficients between seedling traits and mature-plant traits were generally small although nearly half of them were significant (Table 2). Among the seedling traits measured, petiole length had a relatively large and positive correlation coefficient with the mature-plant traits. All the mature-plant traits measured were positively correlated with one another except for IPDW2 and CH3 or IPDW3 and CH2 and YTOT which were not correlated (Table 3). The correlation coefficients among mature-plant traits were usually larger than those between seedling traits and mature-plant traits.

Most seedling traits correlated with mature-plant traits measured in harvest one and two in 1993 were not correlated with mature-plant traits in 1994 (Table 2). The only exceptions were petiole length (correlated to CH3), seedling vigor (correlated to CH3 and VIG3), RLP (correlated to MAT3), and D4LE (correlated to MAT3). Similarly, the value of the correlation coefficients among mature-plant traits decreased over harvests and over the 2 years (Table 3). This type of "time

Table 2 Pearson correlation coefficients between a series of seedling traits, mature-plant traits and forage yields in red clover

Mature-plant trait[e]	Seedling trait[d]									
	Leaves per seedling	Petiole length	Leaflet length	Leaflet width	Seedling vigor	RLP	R2LE	R4LE	D2LE	D4LE
1993										
MAT1[f]	0.173[a]	0.066[a]	−0.003	−0.019	0.044[c]	0.131[a]	0.061[a]	0.105[a]	−0.072[a]	−0.147[a]
VIG1	0.190[a]	0.170[a]	0.146[a]	0.094[a]	0.180[a]	0.129[a]	0.080[a]	0.034	0.008	−0.059[a]
CH1	0.149[a]	0.117[a]	0.054[a]	0.010	0.075[a]	0.114[a]	0.051[a]	0.033[c]	0.004	−0.061[a]
IPDW1	0.211[a]	0.189[a]	0.151[a]	0.159[a]	0.135[a]	0.140[a]	−0.021	0.044	−0.090[b]	−0.165[a]
MAT2	0.164[a]	0.063[b]	−0.012	−0.041[c]	0.050[b]	0.130[a]	0.008	0.066[a]	−0.107[a]	−0.170[a]
VIG2	0.116[a]	0.102[a]	0.047[a]	0.018	0.073[a]	0.088[a]	0.004	0.023	−0.078[a]	−0.126[a]
CH2	0.024	0.161[a]	0.056[a]	−0.011	0.020	0.009	−0.004	0.033	−0.068[a]	−0.074[a]
IPDW2	−0.037	0.129[a]	0.136[a]	0.125[b]	−0.009	0.059	−0.048	−0.039	−0.110[b]	−0.104[b]
Y93	0.121[a]	0.239[a]	0.204[a]	0.196[a]	0.082[b]	0.139[a]	−0.062	−0.010	−0.111[b]	−0.167[a]
1994										
MAT3	0.094	0.034	−0.018	−0.085	0.073	0.126[c]	0.018	0.093	−0.064	−0.124[c]
VIG3	0.077	0.086	0.019	−0.042	0.105[c]	0.066	−0.004	0.076	0.013	−0.041
CH3	0.079	0.127[c]	0.026	−0.018	0.140[b]	0.075	0.017	0.042	−0.047	−0.078
IPDW3	0.059	0.078	−0.012	−0.073	0.083	0.096	0.048	0.088	−0.012	−0.068
YTOT	0.134	0.165	0.096	0.113	0.016	0.186	−0.165	−0.016	0.210	0.075

[a, b, c] Significant at $P = 0.001$, $P = 0.01$ and $P = 0.05$, respectively
[d] RLP = rate of leat production; R2LE and R4LE = expansion rate of the 2nd and 4th leaf; D2LE and D4LE = number of days from emergence to full expansion of the 2nd and 4th leaf
[e] MAT = maturity score; VIG = plant vigor; CH = canopy height; IPDW = individual plant dry weight; Y93 = forage yeild in 1993 and YTOT = total forage yield in 1993 and 1994
[f] Suffix 1, 2, and 3 = harvest 1 or 2 in 1993 and harvest 1 in 1994, respectively

Table 3 Pearson correlation coefficients among the mature-plant traits maturity score (MAT), plant vigor (VIG), canopy height (CH), individual plant dry weight (IPDW), forage yield in 1993 (Y93), and total forage yield in 1993 and 1994 (YTOT) in red clover

Trait[c]	VIG1	CH1	IPDW1	MAT2	VIG2	CH2	IPDW2	Y93	MAT3	VIG3	CH3	IPDW3	YTOT
MAT1	0.532	0.469	0.486	0.515	0.282	0.177	0.231	0.489	0.436	0.179	0.220	0.184	0.488
VIG1		0.644	0.797	0.331	0.438	0.220	0.368	0.774	0.303	0.233	0.261	0.201	0.774
CH1			0.547	0.386	0.306	0.364	0.356	0.619	0.320	0.285	0.379	0.228	0.619
IPDW1				0.377	0.432	0.224	0.458	0.952	0.245[a]	0.318	0.265[a]	0.252[a]	0.953
MAT2					0.534	0.325	0.406	0.461	0.382	0.215	0.215	0.184	0.374[a]
VIG2						0.446	0.765	0.645	0.208	0.179	0.146	0.159	0.619
CH2							0.362	0.318	0.168	0.176	0.277	0.125[b]	0.300[n]
IPDW2								0.707	0.288[b]	0.256[b]	0.193[n]	0.233[n]	0.667
Y93									0.409	0.339[a]	0.281[b]	0.304[b]	0.829
MAT3										0.555	0.457	0.535	0.546
VIG3											0.746	0.841	0.714
CH3												0.600	0.529
IPDW3													0.784

[a, b] Significant at $P = 0.01$ and $P = 0.05$; [n] not significant at $P = 0.05$; all other correlation coefficients were significant at $P = 0.001$
[c] Suffix 1, 2, and 3 = harvest 1 or 2 in 1993 and harvest 1 in 1994, respectively

effect" on correlations was also observed by Bouton (1982) and Simons (1990) in alfalfa and Qiu and Mosjidis (1993) in common vetch.

Variability of the second harvest traits was smaller than those for the first harvest traits in 1993. The coefficients of variability (CV) for MAT2, VIG2, CH2 and IPDW2 were 0.34, 0.38, 0.19 and 0.36 whereas the CV of the corresponding traits MAT1, VIG1, CH1 and IPDW1 were 0.46, 0.46, 0.29 and 0.56, respectively. Therefore, selection progress for first-harvest traits will be expected to be larger than for second-harvest traits.

The mean of the top 10% seedlings for all the traits were different from the corresponding means of the whole population (Table 4). The greatest effect on mature-plant performance was obtained when selection was based upon leaves per seedling, which increased IPDW1 by 23.3% (Table 5). Selection of the 10% seedlings with the greatest petiole length significantly increased IPDW1 by 13.2% and Y93 by 15.7%. Selection for the 10% seedlings with the smallest D4LE (fewer days from emergence to full expansion of the 4th leaf) increased IPDW1 by 15.9% and Y93 by 13.8% (Table 5). Selecting for seedling traits could also affect the distribution of dry matter production in mature plants. For example, selecting for higher seedling vigor could result in an increase of IPDW1 by 21.1% ($P < 0.01$), but a reduction of IPDW2 by 12.3%, although the latter was not significantly different from the mean of the whole population. However, selecting for petiole length, leaflet length or D4LE increased both IPDW1 and IPDW2,

Table 4 Means of the top 10% seedlings for each seedling trait leaves per seedling, petiole length, leaflet length, leaflet width, seedling vigor, rate of leaf production (RLP), expansion rate of the 2nd (R2LE) and 4th (R4LE) leaf, number of days from emergence to full expansion of the 2nd (D2LE) and 4th (D4LE) leaf, compared with the means of the whole population in red clover

Seedling traits	Mean of the top 10% seedling[a]	Mean of the population
Leaves per seedling	6.21 ± 0.48	5.00 ± 0.54
Petiole length	15.08 ± 0.81	11.88 ± 1.88
Leaflet length	3.12 ± 0.47	2.44 ± 0.38
Leaflet width	2.42 ± 0.17	1.90 ± 0.28
Seedling vigor	8.99 ± 0.00	5.20 ± 1.84
RLP	0.26 ± 0.02	0.20 ± 0.02
R2LE	0.98 ± 0.03	0.42 ± 0.12
R4LE	0.55 ± 0.01	0.26 ± 0.05
D2LE	11.76 ± 0.48	14.33 ± 1.65
D4LE	21.61 ± 0.71	24.92 ± 2.09

[a] Means of the top 10% for all the traits are significantly greater than the means of the whole population at $P = 0.001$ (one-tailed t-test)

Table 6 Narrow-sense heritabilities and expected responses to selection under five selection schemes for maturity score (MAT), plant vigor (VIG), canopy height (CH), individual plant dry weight (IPDW), and forage yield in 1993 (Y93) in red clover

Trait[a]	Heritability[b]		Selection method[c]				
	H_1	H_2	1	2	3	4	5
MAT1	0.68	0.85	13.9	17.2	21.9	22.0	24.9
VIG1	0.51	0.74	9.5	11.4	14.0	13.7	15.7
CH1	0.47	0.70	5.7	6.8	8.4	8.1	9.3
IPDW1	0.28	0.72	6.2	7.1	7.9	7.0	7.9
MAT2	0.62	0.82	12.2	14.9	18.8	18.7	21.2
VIG2	0.27	0.68	7.6	8.6	9.6	8.5	9.6
CH2	0.45	0.73	4.6	5.5	6.6	6.3	7.2
IPDW2	0.23	0.43	4.8	5.6	6.5	6.1	7.0
Y93	0.32	0.47	7.1	8.5	10.3	10.0	11.6

[a] Suffix 1 and 2 = harvest 1 or 2 in 1993, respectively
[b] H_1, H_2 = Heritability values on an individual plant basis and on a family mean basis, respectively
[c] 1, 2, 3, 4 and 5 = 10% family selection, 80% among and 12.5% within, 31.6% among and 31.6% within, 12.5% among- and 80% within-family selection, and 10% free (mass) selection, respectively

thus also increasing Y93. These results were in agreement with the correlations measured (Table 2).

The narrow-sense heritability values on individual plant basis ($H1$) for each trait was usually smaller than the corresponding values on a family mean basis ($H2$) (Table 6). The order of heritability values among the traits measured was MAT > VIG > CH > IPDW $\approx$ Y93. Reasonable expected genetic gains were obtained when selecting directly for all mature-plant traits recorded in 1993. The MAT had the greatest expected genetic gain and the highest heritability values. The IPDW had the smallest expected genetic gain and the lowest heritability values. Among the five selection schemes, mass selection was superior to family or any combination of among- and within-family selection except for scheme 3 when selecting for IPDW1 or VIG2, which resulted in the same genetic gain as mass selection. The results obtained in the present study are in agreement with the reports from Aastveit and Aastveit (1990) in meadow fescue (*Festuca pratuca* Hud.) and Charmet and Ravel (1991) in perennial ryegrass (*Lolium perenne* L.) which indicated that additive genetic effects

Table 5 Percentage increases of mature-plant traits and forage yields when selecting the top 10% seedlings for a series of seedling traits, compared with the mean of the whole population for each mature-plant trait in red clover

Mature-plant trait[d]	Population mean (Std)	Seedling trait (%)									
		Leaves per seedling	Petiole length	Leaflet length	Leaflet width	Seedling Vigor	RLP	R2LE	R4LE	D2LE	D4LE
MAT1[f]	3.7 ± 1.7	13.5[a]	0.0	−2.7	−8.1[b]	−5.4	8.1[b]	0.0	−10.8	5.4[c]	8.1[a]
VIG1	5.4 ± 2.5	13.0[a]	11.1[a]	11.1[a]	3.7	9.3[b]	7.4[c]	3.7	−5.6	−3.7	3.0
CH1	44.4 ± 12.7	7.4[a]	2.9[c]	2.9	−0.7	0.0	4.3[c]	1.8	−3.8	−1.6	0.9
IPDW1	119.4 ± 66.4	23.2[a]	13.2[b]	16.3[a]	11.0[c]	21.1[b]	8.2	2.7	−5.3	7.9	15.9[a]
MAT2	4.4 ± 1.5	7.4[a]	3.7	0.0	−3.7[c]	3.7	7.4[a]	0.0	−3.7[a]	5.6[b]	7.4[a]
VIG2	5.8 ± 2.2	6.8[b]	6.7[a]	6.9[c]	−1.7	1.7	5.2	1.7	−1.7	5.2[c]	6.9[b]
CH2	44.2 ± 8.3	0.0	5.2[a]	2.9[a]	−2.0	−2.0	−0.7	0.7	−1.1	2.0[c]	2.3[c]
IPDW2	78.0 ± 28.3	−7.9	8.1	1.9	6.8	−12.3	1.7	4.6	1.9	6.8	3.8
Y93	195.1 ± 82.5	3.8	15.7[b]	11.5[c]	7.5	−1.9	1.0	−0.3	−3.3	7.7	13.8[b]
MAT3	4.1 ± 2.1	14.6	7.3	−7.3	−2.4	2.4	4.9	−4.9	0.0	14.6	14.6
VIG3	5.6 ± 2.9	3.6	16.1	−10.7	5.4	8.9	1.8	3.6	−1.8	−3.6	−1.8
CH3	40.6 ± 13.6	2.5	11.1[c]	−4.9	6.4	5.4	7.6	0.0	−0.7	2.0	4.9
IPDW3	136.0 ± 92.2	1.0	12.1	−15.4	0.1	5.8	3.9	7.6	−3.2	3.6	−8.5
YTOT	288.4 ± 112.3	7.8	18.3	−2.7	−5.0	13.2	7.9	−3.5	2.2	3.4	14.2

[a, b, c] Significant at $P = 0.001$, $P = 0.01$ and $P = 0.05$, respectively
[d] MAT = maturity score; VIG = plant vigor; CH = canopy height; IPDW = individual plant dry weight; Y93 = forage yeild in 1993; and YTOT = total forage yield in 1993 and 1994
[e] RLP = rate of leaf production; R2LE and R4LE = expansion rate of the 2nd and 4th leaf; D2LE and D4LE = number of days from emergence to full expansion of the 2nd and 4th leaf
[f] Suffix 1, 2, and 3 = harvest 1 or 2 in 1993 and harvest 1 in 1994, respectively

Table 7 Indirectly expected responses to selection for individual plant dry weight (IPDW), forage yield in 1993 (Y93), plant vigor (VIG), and canopy height (CH) when selecting the top 10% seedlings for petiole length, number of days from emergence to full expansion of the 4th leaf (D4LE), leaflet length, and leaves per seedling in red clover

Selected trait	Expected response (%)						
	IPDW1[a]	IPDW2[a]	Y93	VIG1	VIG2	CH1	CH2
Petiole length	3.7	1.9	5.0	5.7	1.8	1.4	2.3
D4LE	4.5	0.9	4.4	1.5	1.9	0.4	1.0
Leaflet length	4.6	0.4	3.7	5.7	1.9	1.4	1.3
Leaves per seedling	6.5	−1.8	1.2	6.6	1.9	3.5	0.0

[a] Suffix 1 and 2 = harvest 1 or 2 in 1993, respectively

predominate in the variability within plants of HS families. In fact, mass selection has been an effective breeding method for population improvement in red clover (Taylor and Smith 1979; Bowley et al. 1984).

Indirectly expected responses were calculated for some mature-plant traits when selecting the top 10% seedlings for petiole length, D4LE, leaflet length, and leaves per seedling (Table 7). This was done using the formula $R = h^2S$, where the heritability value (h^2) is $H1$ in our case, S is the selection differential of the mature-plant traits which resulted from selecting the top 10% seedlings for each trait (Table 5). The maximum genetic gain (6.5%) for IPDW1 was obtained when selecting for leaves per seedling whereas the gain when selecting directly for IPDW1 was 6.2% for family selection and 7.9% for mass selection. Substantial genetic gains were also observed for Y93 when selecting for petiole length (5.0%) or D4LE (4.4%), whereas the gain when selecting directly for Y93 was 7.1% for family selection and 11.6% for mass selection. Our results further showed that selection for the other seedling traits was less efficient or useless. These results are in agreement with previous reports showing that the expected gain per breeding cycle, given at the same selection intensity, is less than the gain obtained from direct selection on the target trait (Falconer 1981; Gallais 1983; Magnussen 1991).

In summary, our results indicate that relationships between most seedling traits and mature-plant traits were weak. Nevertheless, selecting seedlings for either petiole length, D4LE, or leaves per seedling produed a superior mature-plant population with higher IPDW1 and Y93. Furthermore, if selection were made on single plants at a developmental stage as early as the fourth seedling leaf or on the petiole length of 5-week-old seedlings, substantial progress of IPDW1 and Y93 could be achieved as indicated by the expected genetic gains. Thus, we can conclude that plants and families with low potential yield can be eliminated at the seedling stage in red clover. This will allow breeders to increase the number of superior plants to be field tested or to conduct a more rigorous evaulation of the selected plants. Among the five selection schemes tested for direct selection of mature-plant traits, mass selection produced the largest genetic gain.

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