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Vigour evaluation for genetics and breeding in rose

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Summary

Breeding of cut and pot rose cultivars for efficient production under low-energy conditions in greenhouses will be facilitated by understanding the inheritance of vigour. To get insight into the genetic variation of vigour-related traits, a diploid rose population was employed for an evaluation study in greenhouses in The Netherlands and Denmark. For all the traits investigated the population showed a continuous quantitative variation as well as a considerable transgression. For most of the traits, the genetic variation found among the tested entries was highly significant and tended to be large in comparison to the effects of genotype by environment interaction. The heritability based on means of the traits was high and ranged from 68 to 92%. Strong simple correlations ($r = 0.65$ to 0.95) were found among the traits shoot length, leaf area, leaf dry weight, stem dry weight, total dry weight and growth rate. The total dry weight and leaf area are suggested to be good parameters for early selection of rose genotypes with vigorous growth under suboptimal growth conditions.

Introduction

Energy is a significant factor in the production costs for cut and pot rose producers in Northern Europe, where the crops are cultivated in greenhouses all the year around and require, especially in the winter season, supplementary heat and light to reach optimal growth and flower production. In addition, growers are confronted with an increasing political pressure to reduce the CO_2-emission resulting from greenhouse production. For example, in 1997 an agreement was reached between Dutch growers and the Dutch government to improve the efficiency of energy use in greenhouse production by 65% in 2010 compared to 1980 (Korner, 2003). To reach this goal, both technical improvements of greenhouse production systems and genetic crop improvements are pursued. Energy efficiency of greenhouse cultivation is the ratio of energy fixed in biomass and the amount of energy needed for plant production. This can be improved through better light interception, cultivation methods, crop varieties and CO_2 enrichment (Van der Velden, 1992).The development of new cultivars with a higher production per unit energy input requires criteria for selection to facilitate breeding. This implies that such criteria should be simple to assess and should comprise all or at least most of relevant component traits of vigour.

The choice of selection strategy breeding for crop improvement requires at least some knowledge of the inheritance of the major target traits (Debener, 2003). In rose, however, the genetic knowledge is still limited and research certainly does not match its economical importance. This is partly due to the complex genetic nature of rose cultivars, including polyploidy,

self-incompatibility, low seed set, poor seed germination and a high degree of heterozygosity. Nevertheless, rose geneticists have started to unravel the inheritance of some morphological and physiological traits. As reviewed by Gudin (2000) and Debener (2003), monogenic inheritance was found for traits such as recurrent flowering, prickles on stems and petioles, flower colours yellow and pink, double flowers, double corolla, dwarfing, moss phenotype, resistance to black spot and powdery mildew. In addition, polygenic inheritance was found for winter hardiness, number of petals, and thorn density on shoots (Crespel et al., 2002). Little, however, is known to date on characteristics that determine the productivity of rose under suboptimal conditions, like vigour and adaptation to a low energy environment (De Vries et al., 1980; 1982; De Vries & Dubois, 1996).

Proper evaluation methods for assessment of phenotypic traits relevant to the energy efficiency of crops are needed for genetic improvement. Temperature is one of the climatic factors to be considered to optimize selection of rose cultivars to be used in energy saving greenhouses, together with factors as light and air humidity (Berninger & Philouze, 1988). De Vries et al. (1982) conducted an experiment with 15 Hybrid tea rose F1 populations in nine growth conditions, i.e. combinations of three light levels of 8, 16, 24 Wm^{-2} (visible) irradiation and three temperatures of 16, 20 and 24 °C, and concluded that the effects of temperature on shoot growth were basically the same under high and low light intensity; temperature and light were independent factors, which suggested that genotypes adapted to both low light and low temperature might be selected under the test regimes. In an earlier study, De Vries et al. (1980) evaluated seedlings from 30 Hybrid tea rose F1 populations in greenhouse at six constant temperatures (10, 14, 17, 20, 23 and 26 °C) under natural light conditions. The results of these studies suggested that temperatures about 3 °C lower than normal (∼23 °C) in greenhouse cultivation are the best for selection of energy-efficient genotypes.

Vigour is a poorly defined and complex trait that is likely to be controlled by numerous elementary genetic factors. Therefore, a direct genetic analysis is difficult and usually not very rewarding. A common strategy to circumvent this is to dissect a complex quantitative trait into its underlying components and study their genetics component by component (Rami et al., 1998; Xu, 2001). The basic assumption is that the component traits are easier to be determined and have a relatively simple inheritance (Xu, 2001).

The objective of the current study was to elaborate a simple procedure for testing vigour of roses and to use this screening method for the evaluation of a variable diploid rose population for traits related to vigour under suboptimal growth conditions. The testing method developed was based on re-growth of single secondary shoots on rooted cuttings, and its efficiency as well as the importance of genotype by environment interactions was evaluated in the experiments under controlled conditions at different geographic locations. The implications of the results for early selection in breeding genotypes with a higher production per unit energy input will be discussed.

Materials and methods

Plant materials

The genotypes used in this study consisted of 88 diploid rose plants of population 94/1, and its two parents, 93/1-119 (P119) and 93/1-117 (P117), which were derived from *R. multiflora* (Debener & Mattiesch, 1999). The same population has been used previously to develop a fairly dense genetic map of rose (Yan et al., 2005). Rooted cuttings of each genotype were produced under commercial conditions from mother plants of the same age. The number of cuttings per entry was in excess to allow some selection for uniform starting materials. Each cutting was allowed to produce a single shoot from one axillary bud and the others were removed. When the shoots were about 5 cm in length, the cuttings were transplanted from trays into 10 cm^2 pots with commercial potting soil, and transferred to the testing rooms with conditions designed for the experiment. When the first shoot had reached the stage of forming a visible flower bud, the shoot was cut back to the first internode of the first shoot, leaving again only one basal axillary bud to form a second shoot. A final selection of uniform plants was performed before evaluation at the stage that the second shoots had reached a length of about 5 cm.

Pilot experiment

Eleven genotypes differing in vigour were selected from the diploid rose population and were used, together with both parents of the population, to conduct a pilot experiment for vigour. The experiment was carried out in two phytotron rooms (Smeets, 1978) set at 16 °C and 20 °C, respectively. The photoperiod was

set at 20 h light/4 h dark and light intensity at canopy level in both rooms was about 120 μmol m^{-2} s^{-1}. Relative humidity was kept between 60 and 70%. Just after removal of the first shoots, the plants were placed according to a randomized block design with three replications and five pots as an experimental unit (plot).

Population evaluation

The entire population was evaluated in greenhouse experiments in Fredensburg, Denmark, in October 2002 (DK) and in Wageningen, The Netherlands, in March 2003 (NL). Only one temperature condition was used. Growth conditions were kept similar at both experimental sites: the set was temperature 20 °C and lowered by 2 °C during the dark period, and light intensity 120 μmol m^{-2} s^{-1} with a period of 16 h per day. The experimental design was similar to that of the pilot experiment.

Vigour-related traits

In the pilot and population studies, ten vigour-related traits were measured on the shoot of individual plants when the flower buds of the shoot reached a length of 0.6 cm. The traits were: number of internodes, shoot length, stem thickness, chlorophyll content, shoot leaf area, leaf dry weight, stem dry weight, total dry weight, specific leaf area and absolute growth rate. The codes used for the traits are indicated in Table 1. Chlorophyll content was measured on the lowest three leaves with a Minolta SPAD-520 chlorophyll meter (Minolta, Ramsey, NJ, USA). Leaf area was measured on collected leaves of the shoot with a leaf area meter (Li-Cor 3100, NEB, Lincoln, USA). Leaf and stem dry weights were determined after drying for 24 h in an oven at 80 °C. Specific leaf area was the ratio of leaf area and leaf dry weight. Growth rate was calculated by dividing the total dry weight of the second shoot at harvest by the growth period of the shoot (number of days from the moment the first shoot was cut until the second shoot was harvested).

Data analysis

For each trait and each experiment the distribution of mean trait values were inspected. GenStat version 6.1 (Payne et al., 2002) was used to perform analyses of variance for the pilot study, the two evaluation studies of the population, as well as a combined analysis of the latter studies. Mean comparison, the computation of broad-sense heritability and correlation coefficients between the traits were conducted. Heritability of the trait was calculated based on plot means by $h^2 = \sigma_g^2/(\sigma_g^2 + \sigma_e^2/r)$ for an individual experiment, and by $h^2 = \sigma_g^2/(\sigma_g^2 + \sigma_{gl}^2/l + \sigma_e^2/rl)$ for joint data from both experiments, where, σ_g^2 represents the genetic variance, σ_{gl}^2 the variance due to genotype by experiment interaction (G × E), σ_e^2 the error variance, r the number of replications and l the number of experiments.

Results

Pilot experiment

In the pilot experiment, vigour was studied under two growth conditions, i.e. at 16 °C and 20 °C. The results are summarized in Table 2. Highly significant genotypic differences ($P < 0.01$) were found for all the

Table 1. Description of vigour-related traits evaluated in diploid 94/1 population

Vigour-related trait	Code	Unit	Description of measurement
Number of internodes	NI		Number of extended internodes at harvest
Stem thickness	ST	mm	Diameter of the stem at middle of the 2nd internodes from shoot basis
Shoot length	SL	cm	Length from the top to the shoot basis
Chlorophyll content	CC	mg/l	Measured on the lowest three leaves of a plant with a meter
Leaf area	LA	cm^2	Area of all shoot leaves including petiolule and leafstalks
Specific leaf area	SLA	cm^2/g	Ratio between leaf area and leaf dry weight
Leaf dry weight	LDW	g	Dry weight of leaves including petiolule and leafstalks
Stem dry weight	SDW	g	Dry weight of stem, excluding leaves, petiolule and leafstalks
Total dry weight	TDW	g	Sum of leaf dry weight and stem dry weight
Growth rate	GR	g/day	Ratio between total dry weight and growth period

Table 2. Variance analysis and means of nine selected entries of the diploid population and its parents (P119 and P117) in a pilot experiment performed under two temperature regimes

	Mean at 16 °C			Mean at 20 °C			*F* value	
Trait	P119	P117	Range progeny	P119	P117	Range progeny	Genotype	GxE
NI	7.47	7.33	4.93–9.07	7.92	7.85	6.05–9.02	37.11**	6.11**
ST	2.10	1.96	1.57–2.53	2.30	2.10	1.64–2.46	33.46**	4.29**
SL	22.21	22.57	11.59–30.37	23.34	23.57	15.77–25.39	61.94**	6.94**
CC	40.24	38.51	36.77–46.69	42.17	42.55	35.87–44.15	14.05**	2.34 *
LA	155.40	118.00	67.90–189.50	162.40	140.60	78.70–169.00	24.59**	3.06**
SLA	366.10	251.40	254.00–386.80	306.50	314.90	297.60–332.70	2.73*	3.15**
LDW	0.66	0.52	0.17–0.91	0.83	0.61	0.34–0.78	24.37**	4.42**
SDW	0.27	0.28	0.07–0.44	0.35	0.25	0.17–0.46	20.82**	5.03**
TDW	0.94	0.81	0.21–1.33	1.19	0.79	0.52–1.16	20.32**	4.02**
GR	0.04	0.03	0.02–0.04	0.05	0.03	0.01–0.05	13.53**	3.14**

Codes of traits are given in Table 1. Significance of variances among genotypes (G) and genotype by environment interaction (G × E) are indicated with *, ** at the 0.05 and 0.01 levels of probability, respectively.

traits except for SLA ($P < 0.05$). Interactions between genotype and growth environment were also found to be significant, indicating that relative performance of entries was temperature dependent. However, the magnitude of the interaction component was small compared to the genetic variance.

The parents of the mapping population had a stronger growth at 20 °C than at 16 °C, whereas they also differed considerably from each other as well as from the selected offspring for most of the traits. The parent P119 was more vigorous in growth than P117 under both conditions. For all the traits, the range of means of the tested progeny was much broader at 16 °C than at 20 °C (Table 2). However, the performance of each genotype at both temperatures was highly correlated (data not shown). At 16 °C, plants had longer growth periods, and thus ended up with lower growth rates (Table 2).

Greenhouse evaluation of the population

The frequency distribution of the mean performance and the population entries are shown trait by trait for each location (Figure 1). All traits showed a more or less normal and continuous distribution. The variation range among entries was much wider than the difference found between the parents, indicating the presence of transgressive segregation. The distributions of the population for different traits in NL and DK were quite similar and had an approximately equal range. However, the population means varied from trait to trait, for example, a higher population mean for ST, SL, SLA, SDW, TDW and GR was recorded in the DK experiment, indicating the growing conditions were somewhat better in the Danish experiment.

Means and variance components were also obtained from the analyses of variance using the combined data from the two greenhouse experiments (Table 3). The parents differed much for all traits, except for NI and SLA (Figure 1; Table 3). The means of P119 were generally higher than those of P117, similarly as observed in the pilot study. In most cases, the overall means of the population was between the parental values (Figure 1; Table 3). The analyses of the separate experiments as well as the overall analyses showed highly significant differences among entries ($P < 0.01$) for all the traits. The G × E interaction was also significant for all the traits except for SLA (Table 3). In all cases, however, its magnitude was much smaller than that of the factor genotype. The variation for most traits assessed in the experiments was highly heritable. The broad-sense heritability estimates based on plot means ranged from 68 to 92% in individual experiments (Figure 1). The estimates based on the entry means over experiments ranged from 48 to 72% (Table 3). The estimates from the combined analyses tended to be somewhat lower than those from the corresponding separate analyses. However, the three estimates with different sets of data for a trait showed the same tendency.

Simple correlation coefficients were calculated for all pair-wise combinations of trait means for both

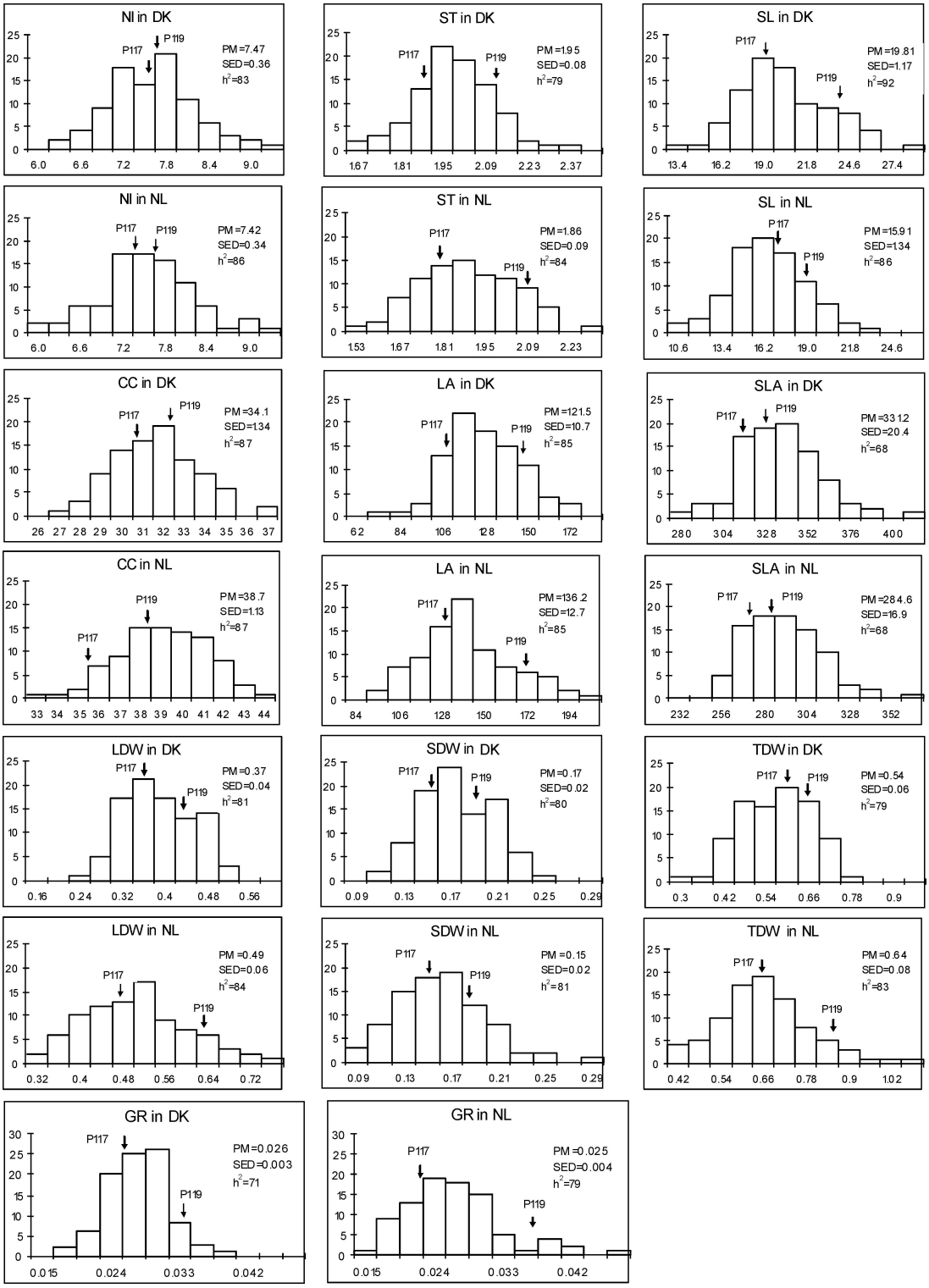

Figure 1. Distribution of vigour-related traits measured on 88 entries of the diploid population evaluated separately in Denmark (DK) and The Netherlands (NL). The means of parents P119 and P117 are indicated by arrows. Population mean (PM), standard error of difference of means (SED) and broad-sense heritability (h^2, %) are shown. Codes for traits are given in Table 1.

Table 3. Estimates of means, variance components and heritabilities of vigour-related traits evaluated in the diploid population using combined data of the experiments carried out in Denmark and The Netherlands

	Means					Variance components			
Trait	P119	P117	Population	Range	S.E.D.	σ_g^2	σ_{gl}^2	σ_e^2	h^2 (%)
NI	7.67	7.50	7.44	6.21–9.10	0.25	0.223**	0.121**	0.186	71
ST	2.09	1.85	1.91	1.61–2.33	0.06	0.011**	0.005**	0.011	71
SL	18.69	20.45	17.87	12.86–25.04	0.89	4.377**	2.663**	2.39	72
CC	33.97	34.69	34.92	29.88–38.84	0.88	1.900**	1.651**	2.32	61
LA	157.9	122.2	128.9	88.8–175.4	8.30	209.00**	180.80**	207.3	63
SLA	298.4	300.9	307.9	267.9–364.6	13.20	290.00**	68.79ns	628.8	67
LDW	0.54	0.42	0.43	0.29–0.65	0.03	0.0034**	0.0025**	0.004	65
SDW	0.17	0.17	0.16	0.11–0.23	0.02	0.00052**	0.00043**	0.0007	62
TDW	0.71	0.59	0.59	0.40–0.87	0.05	0.0060**	0.0047**	0.007	63
GR	0.03	0.02	0.03	0.018–0.036	0.003	0.000007**	0.000015**	0.00002	48

Codes of traits are given in Table 1. S.E.D. indicates standard error of difference of means. * and ** indicate significance at the 0.05 and 0.01 levels of probability, respectively. σ_g^2, σ_{gl}^2 and σ_e^2 are variance components for genotype, genotype by experiment interaction and error, respectively. Broad-sense heritability (h^2, %) was estimated on plot means by $h^2 = \sigma_g^2/(\sigma_g^2 + \sigma_{gl}^2/2 + \sigma_e^2/6)$.

experiments (Table 4). The estimates for corresponding combinations in the two experiments were fairly similar (Table 4). The morphological traits NI, ST and SL were moderately correlated ($r = 0.52$ to 0.66). Strong positive correlations ($r = 0.67$ to 0.95) were observed for the traits describing the dry matter allocation, i.e. LDW, SDW and TDW. The photosynthesis-related traits CC, LA and SLA, on the other hand, showed a weak relation ($r = -0.10$ to 0.25). The morphological traits were moderately related with other traits except SLA and CC. The relationship of SLA with other traits was practically absent to medium ($r = -0.06$ to -0.50). Trait CC had positive low and intermediate relations with other traits except SLA ($r = 0.12$ to 0.33). High correlations ($r = 0.65$ to 0.95) were found among LA, LDW, SDW, TDW and GR.

Discussion

Vigour is an important agronomic trait in crop improvement. Genetic studies on vigour and related traits have been performed in a wide range of plant species like sorghum (Cisse & Ejeta, 2003), wheat (Regan et al.,

Table 4. Correlation coefficients of vigour-related traits of the diploid population evaluated in experiments carried out in Denmark (DK; upper left) and The Netherlands (NL; lower right) under similar conditions. Codes of traits are given in Table 1.

Trait	GR	TDW	SDW	LDW	SLA	LA	CC	SL	ST	NI
NI	0.35	0.49	0.53	0.41	−0.06	0.46	0.18	0.59	0.54	–
ST	0.56	0.60	0.61	0.52	−0.13	0.55	0.12	0.52	–	0.61
SL	0.50	0.67	0.81	0.53	−0.13	0.57	0.22	–	0.66	0.63
CC	0.20	0.32	0.29	0.32	−0.38	0.18	–	0.32	0.15	0.16
LA	0.76	0.84	0.66	0.85	−0.10	–	0.25	0.77	0.72	0.63
SLA	−0.38	−0.43	−0.24	−0.50	–	−0.13	−0.26	−0.28	−0.25	−0.22
LDW	0.86	0.94	0.67	–	−0.48	0.90	0.33	0.78	0.72	0.62
SDW	0.65	0.83	–	0.85	−0.34	0.79	0.30	0.84	0.69	0.60
TDW	0.85	–	0.92	0.95	−0.46	0.90	0.33	0.82	0.74	0.63
GR	–	0.95	0.91	0.93	−0.35	0.87	0.27	0.83	0.71	0.57

1992), rice (Redona & Mackill, 1996; Cui et al., 2002), maize (Revilla et al., 1999), chickpea (Sabaghpour et al., 2003) and willow (Tsarouhas et al., 2002). Vigour is a complex plant characteristic that usually is reflected in the variation of plant traits, such as leaf number, leaf size, leaf area, leaf weight, plant height, plant weight, root weight, etc. The present study was focussed on the development of a simple procedure to test plant vigour using one single growing shoot per cutting. According to breeders, the evaluation on second shoots would yield the most useful results since in cut rose production these secondary shoots form part of the backbone of the plants and produce the first saleable flowering lateral shoots. Cuttings for pot rose production are also cut back twice before allowing them to flower. In the testing method developed, ten vigour-related components were evaluated on the second shoot of rooted rose cuttings. Random variation was minimized by the procedures followed during pre-treatment of plant materials, standardization of the starting plant materials at the onset of an experiment and the design of the experiments. The studies in this way showed that data for vigour-related components could be collected in a fairly short period of time, for example, about one month in the present study.

A diploid population derived from the wild species *R. multiflora,* one of the ancestors of cultivated tetraploid roses, was used. The reason for employing a diploid population instead of a tetraploid population is to prevent the complexity of tetrasomic inheritance since after this study a molecular analysis of inheritance of the component traits of vigour is envisaged. Therefore, the component analysis of vigour presented here should be considered as a first step to obtain the required data needed for this purpose. The marker analysis will finally pave the way towards marker-assisted selection for vigour in rose breeding at the tetraploid level. This strategy has been used successfully in similar genetic studies on other polyploid species such as potato and alfalfa (Bonierbale et al. 1988; Hamalainen et al., 1997; Gehardt & Valkonen, 2001; Bryan et al., 2002; Echt et al., 1993). The present population may harbour some promising genes or alleles for vigour which may not be present in modern rose cultivars. These genes, however, have to be unlocked before they can be used for genetic improvement of modern tetraploid roses. This can be done by doubling of the chromosome number of the diploid genotype and crossing with tetraploids. The progeny of such crosses could be used subsequently as starting material for marker-assisted selection.

A small scale pilot experiment under two different growth conditions and two large scale experiments in greenhouses at one temperature condition revealed significant genetic differences among tested entries of the population for vigour-related traits as well as the presence of G $\times$ E interactions. However, the magnitude of the latter was much smaller than the genetic variation. The large genetic variation for vigour-related traits was indicated by differences in performance of the parents for most of the traits and by the observed transgression in the population. A continuous frequency distribution of the entry means for all vigour-related traits together with a transgressive segregation was observed, suggesting a polygenetic inheritance of the traits (Hartl, 1980). The results of these studies suggested that a temperature 20 °C, which is about 3 °C lower than normal ($\sim$23 °C) in greenhouse cultivation, is suitable for selection of energy-efficient genotypes. This is in agreement with the findings of De Vries and co-workers (1980, 1982).

The current study demonstrated that total shoot dry weight, an important part of biomass production, is largely dependent on leaf dry weight ($r = 0.94$ to 0.95), stem dry weight ($r = 0.83$ to 0.92), leaf area ($r = 0.84$ to 0.90) and partly dependent on number of internodes ($r = 0.49$ to 0.63), shoot thickness ($r = 0.60$ to 0.74) and shoot length ($r = 0.67$ to 0.82). A similar magnitude of relationship existed for growth rate with the above-mentioned vigour components. It is obvious that leaf area, rather than specific leaf area (leaf thickness) and chlorophyll content, contributed most to biomass accumulation, suggesting that leaf area, total dry weight and growth rate are key traits to examine vigour in rose breeding programs. However, growth rate has a relatively low heritability in the present study. Therefore, total dry weight and leaf area are suggested to be good parameters for early selection of genotypes with vigorous growth under suboptimal growth conditions. Further studies are needed to find out whether the observed prominent correlations are due to pleiotropy or linkage. A validation of the findings in the present study also needs to be performed in a tetraploid population.

Due to practical limitations, neither root production nor branching capacity of the genotypes was evaluated in this study, although both characteristics were shown to influence rose flower production (Fuchs, 1994; De Vries, 1993), and are possibly correlated with vigour. A sound root system usually is a prerequisite for a strong shoot formation and a large flower production (De Vries, 1993; Kool, 1996). Physiological studies on

rose have revealed close relationships among root dry weight, shoot dry weight and flower production (Hu, 2001; Costa, 2002).

A large amount of genetic variation together with a high heritability was found for most of the examined vigour-related traits. Based on these results, it is realistic to start a breeding program for vigour. To this end, molecular markers associated with vigour QTLs are helpful. Therefore, the next step of this study will be the identification of QTLs for each of the ten vigour-related traits described in this paper with help of the molecular linkage map of Yan et al. (2005). The localization of these QTLs will offer the possibility to select separately for individual components of vigour in rose. In addition, it will facilitate the introgression of favourable alleles from the wild species *R. multiflora* into cultivated roses (Tanksley & McCouch, 1997; Stam, 2003).

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