Plant and Soil (2005) 272: 11–27
DOI 10.1007/s11104-004-3846-8

Variation in relative growth rate of 20 *Aegilops* species (Poaceae) in the field: The importance of net assimilation rate or specific leaf area depends on the time scale

Rafael Villar[1,5], Teodoro Marañón[2], José Luis Quero[1,3], Pilar Panadero[2], Francisco Arenas[2] & Hans Lambers[4]

[1]*Area de Ecología, Facultad de Ciencias, Universidad de Córdoba, 14071 Córdoba, Spain.* [2]*IRNA, CSIC, Apartado 1052, 41080 Sevilla, Spain.* [3]*Departamento de Biología Animal y Ecología, Facultad de Ciencias, Universidad de Granada, Granada, Spain.* [4]*School of Plant Biology, Faculty of Natural and Agricultural Sciences, The University of Western Australia, Crawley WA 6009, Australia.* [5]*Corresponding author**

Received 26 May 2004. Accepted in revised form 27 September 2004

Key words: biomass allocation, growth analysis, leaf area ratio, RGR, SLA, wild wheat

Abstract

Field experiments reporting the relative growth rate (RGR) patterns in plants are scarce. In this study, 22 herbaceous species (20 *Aegilops* species, *Amblyopyrum muticum* and *Triticum aestivum*) were grown under field conditions to assess their RGR, and to find out if the differences in RGR amongst species were explained by morphological or physiological traits. Plants were cultivated during two months, and five harvests (every 13–19 days) were carried out. Factors explaining between-species differences in RGR varied, depending on whether short (13–19 days) or longer periods (62 days) were considered. RGR for short periods (4 growth periods of 13–19 days each) showed a positive correlation with net assimilation rate (NAR), but there was no significant correlation with leaf area ratio (LAR) (with the exception of the first growth period). In contrast, when growth was investigated over two months, RGR was positively correlated with morphological traits (LAR, and specific leaf area, SLA), but not with physiological traits (NAR). A possible explanation for these contrasting results is that during short growth periods, NAR exhibited strong variations possibly caused by the variable field conditions, and, consequently NAR mainly determined RGR. In contrast, during a longer growth period (62 days) the importance of NAR was not apparent (there was no significant correlation between RGR and NAR), while allocation traits, such as LAR and SLA, became most relevant.

Introduction

The relative growth rate (RGR; mass increase per unit time and mass) of plants is determined by their genetic background and by environmental conditions. The inherent variation in RGR, and the associated suite of traits, helps to explain the ecological performance of plants (Grime and Hunt, 1975; Lambers and Poorter, 1992; Lambers et al., 1998; Poorter and Garnier, 1999).

During the last decades there has been an increasing interest to determine the potential RGR (RGR_{max}) of plant species, and to find out whether the differences in RGR_{max} amongst species are mainly caused by morphological or by physiological traits. Most of these studies have been carried out under controlled conditions

* E-mail: bv1vimor@uco.es

(laboratory or greenhouse) which has the clear advantage of estimating the RGR_{max} and to identify the causes of its variation amongst species under standard conditions. In such studies, under uniform and near-optimum conditions, the interspecific RGR_{max} differs several-fold (10–400 mg g^{-1} day^{-1}, Poorter and Garnier, 1999). This wide variation in RGR amongst species has been explained mainly by plant morphological variables, such as leaf area ratio (LAR) and specific leaf area (SLA) (e.g., Atkin et al., 1996; Cornelissen et al., 1996; Garnier, 1992; Marañón and Grubb, 1993; Poorter and Garnier, 1999; Poorter and Remkes, 1990; Van den Boogaard et al., 1996). SLA is considered a major factor associated with variation in RGR (Lambers et al., 1998).

What happens under field conditions? In the few field growth studies, it has been found that plant features and growth patterns are strongly affected, and the species' RGR_{max} is rarely attained (Garnier and Freijsen, 1994). Under natural conditions, the environment is very different from that experienced under controlled, laboratory experiments, and, consequently, the plant responses, in terms of growth and biomass allocation, also vary (Garnier and Freijsen, 1994; Poorter and Garnier, 1999). For example, under field conditions water or mineral nutrient resources may be limiting; light and temperature fluctuate, reaching values well above or below the optimum for plant growth. All of these limitations constrain the RGR of plants growing under field conditions.

Environmental conditions determine both the realised RGR and the relative importance of the growth components. Two recent studies have challenged the general view of SLA as the major determinant of RGR. Shipley (2002) has demonstrated that the mean daily photon flux is very relevant to explain the causes of the RGR differences between species. Thus, at high daily photon flux density, variation in RGR was strongly and positively correlated with net assimilation rate (NAR), but weakly and negatively with SLA. Shipley (2002) argued that the commonly reported result that "the interspecific variation in RGR is determined primarily by SLA", is partly due to the low irradiance used in most experiments. Therefore, the relative importance of SLA and NAR would change depending on the irradiance perceived by the plant. In another study, Loveys et al. (2002) found that RGR was significantly and positively correlated with NAR, when plants were cultivated at 18 °C. However, when growth temperature was increased (to 23 or 28 °C), the RGR pattern switched, and correlated positively with SLA, but not with NAR.

In spite of the importance of studying growth under natural conditions, there are only a few studies investigating the growth patterns and related traits (such as LAR, SLA, biomass allocation and NAR) of wild plant species growing either in natural habitats or cultivated under field conditions. The two approaches used in growth studies: experiments with controlled environments and field studies are both valid and complementary. However, there is a considerable gap in growth studies under natural conditions and for that more studies are needed to be able to make generalisations.

In this study, 20 *Aegilops* (wild wheat) species, plus *Amblyopyrum muticum* (formerly *Ae. mutica*) and *Triticum aestivum* L. cv. Yecora (wheat) were cultivated under similar field conditions. The *Aegilops* genus (with 22 annual species) naturally occurs in the Mediterranean region, and Western and Central Asia (Van Slageren, 1994). The species vary in level of ploidy (diploid, tetraploid and hexaploid), and are found in habitats with different annual rainfall (75–1400 mm) and altitude (from 400 m b.s.l. in the Dead Sea area, to up to 2700 m a.s.l.) (Van Slageren, 1994). This group of species has agronomic interest, because some of them have contributed to the genome of modern wheat species (*Triticum*), and they might be a source of valuable traits for future wheat cultivars (Lambers et al., 1995), to improve grain quality, disease resistance, heat and cold tolerance, photosynthetic rates, early vigour, and micronutrient acquisition (Cakmak et al., 1999; García et al., 1997; Van den Boogaard and Villar, 1998).

The objectives of this study were (1) to estimate the RGR of the 20 *Aegilops* species, as well as *Am. muticum* and *T. aestivum*, under common field conditions; (2) to determine which are the variables more associated with the variation in RGR amongst species, under those field conditions; and (3) to analyse the

temporal changes in RGR during the vegetative stage.

Material and methods

Seeds of *Aegilops* and *Amblyopyrum* were obtained from ICARDA (International Center for Agricultural Research in Dry Areas, Aleppo, Syria); they were collected at different locations in the Mediterranean area, Middle East and Central Asia. Data on altitude and annual rainfall of the place of origin of the seeds were provided by ICARDA. Nomenclature follows Van Slageren (1994). Seeds of *T. aestivum* L. cv. Yecora were obtained from a local company in Seville (Spain).

Plants of the *Aegilops* genus produce heteromorphic seeds (Marañón, 1989); within the same plant progeny they may have different mass, colour, germination percentage and germination time. To reduce variation in the time of germination and the initial seedling mass, we discarded the smaller and darker seeds, which need more time to germinate and have a smaller initial seedling mass. Seeds were placed in Petri dishes with a wet filter paper at 4 °C, and kept in darkness for one week. Then, seeds were placed in a growth chamber for 4 days at 25 °C and a 16 h photoperiod (30 μmol m^{-2} s^{-1}). After germination, seedlings were placed in a greenhouse, in a container (40 × 20 cm) filled with a bulk sample of soil from the field plot. To homogenise the initial seedling mass and to have a more precise estimate of RGR (Poorter and Garnier, 1996), we selected a batch of 100 seedlings with similar size within each species (approximately with three leaves and 7 cm high). Seedlings were removed from the soil before transplanting into the field; the few plants that, after two or three days of transplanting, suffered damage were discarded. The transplant task lasted from January 19 to February 1, 1995.

The field plot had about 600 m^2 and was located in the experimental station "La Hampa" (Coria del Río, Seville, Spain) belonging to CSIC (Consejo Superior de Investigaciones Científicas). The rainfall pattern during the two-months growth period (Figure 1c) was relatively dry (66 mm), 53% of the long-term average for 1972–1999. Values (mean ± SD) of maximum temperatures were 20.8 ± 3.8 °C and of minimum temperatures were 7.9 ± 2.9 °C; there was a positive correlation of both maximum and minimum temperatures with day in the year ($r = 0.82$; $P < 0.001$ and $r = 0.50$; $P < 0.001$, respectively; Figure 1b). The mean daily photosynthetic photon flux density was 29.6 ± 11.4 mol m^{-2} (Figure 1a). There was also a positive correlation of mean daily photon flux density with day in the year ($r = 0.81$; $P < 0.001$).The mean relative air humidity in the morning at 7 h was 92 ± 12%, and in the evening at 18 h it was 53 ± 23% (Figure 1d).

Before the transplant, the field soil was prepared by ploughing and harrowing at 30 cm depth, and fertilised with urea (15 g m^{-2}). To avoid a confounding effect by the possible spatial heterogeneity of the soil, we planted the seedlings of the different species with a completely random design. Each plant was separated from the nearest neighbour by 0.5 m. Just before planting (January 16th), the plot was irrigated (3.6 L m^{-2}) to improve the establishment of the seedlings. Also, during planting, each individual received about 50 mL of water. In spite of being a relatively dry year (compared with the long-term average), almost all the seedlings survived and grew up to maturity.

Five harvests were carried out during the vegetative growth period, with intervals of 13–19 days. The timing for all the species was as follows (mean ± SD): harvest 0 (initial) on day 0 ± 5; harvest 1 on day 14.1 ± 1.4; harvest 2 on day 30.4 ± 2.8; harvest 3 on day 43.4 ± 2.3; and harvest 4 on day 62.0 ± 5.6. That is, a total of five harvests determining four growth periods, each one lasting about 13–19 days (specifically, 14, 16, 13 and 19 days). For two species (*Ae. searsii* Feldmann and Kislev ex Hammer and *Ae. crassa* Boiss) the 3rd harvest could not be carried out, because there were not enough seedlings.

At every harvest, 8 individuals of each species were selected at random. Each plant was carefully excavated with a shovel, at 30 cm depth, and then the soil was washed off its roots. Immediately the plant was separated into leaves, stems (including the leaf sheaths) and roots. The fresh weight of each fraction was

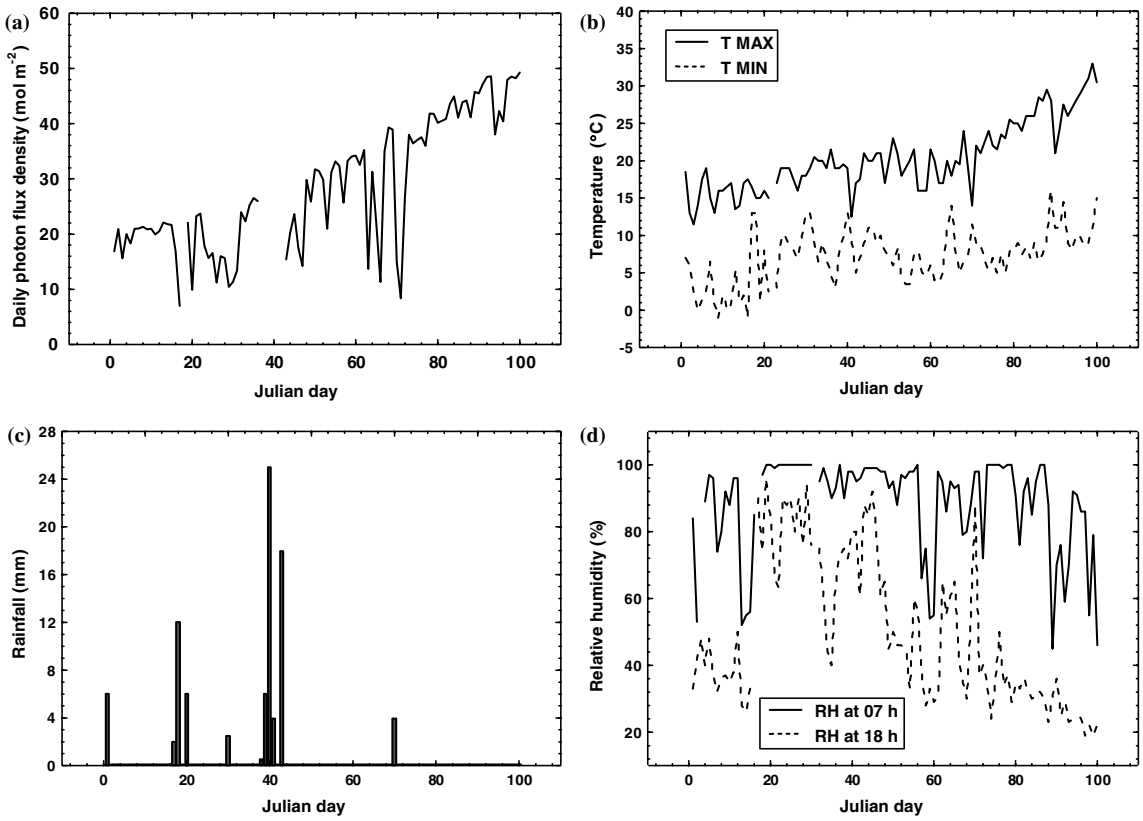

Figure 1. (a) Mean daily photosynthetic photon flux density, (b) daily maximum and minimum temperature, (c) rainfall and (d) relative humidity of the air in the morning (at 7 h) and the evening (18 h), in the experimental station "La Hampa" (Coria del Río, Seville, Spain) during the studied period of growth.

measured at once. Leaf area was measured using an image analyser (SKYE Instruments, Ltd., Powys, UK). Dry mass was determined from material oven-dried at 70 °C for at least 48 h. Leaf N concentration of plants at harvest 5 was determined with a modified Kjeldahl analysis using concentrated sulphuric acid and Na_2SO_4, K_2SO_4 and Se in a ratio of 62:1:1 (w/w) as a catalyst.

Growth analyses were carried out separately for the four short-term (2–3 weeks) growth periods. The analyses of the data followed the classical approach, for that we used the excel file published in Hunt et al. (2002; http://www.ex.ac.uk/~rh203/growth_analysis.html) which incorporates the approach of Hoffmann and Poorter (2002).

The average values for the long-term (two-months) growth period were calculated as the mean values of the four growth periods.

Additionally, all the data were also analysed using the functional approach (Hunt and Parson, 1974); specifically with the free program Hp curves (http://www.ex.ac.uk/~rh203/growth_analysis.html). The results (not shown) were very similar to those obtained with the classical approach and presented in this paper.

The growth rate components (GRC) were calculated according to Poorter and Van der Werf (1998), as the slopes estimated from a linear regression where ln LAR, ln NAR, ln SLA and ln LMR were the dependent variable, while ln RGR was the independent variable.

For all the statistical analyses, the whole set of 22 species (20 *Aegilops*, *Ambliopyrum* and *Triticum*) was considered. For the correlation and regression analyses, for RGR and the other growth parameters, the results were similar whether the cultivated wheat (*Triticum*) was included in the analyses or not. Thus, all the

results presented here include *Triticum*. The relationships between RGR and other growth variables for the 22 species were analysed by correlation and linear regression using Statistica for Windows, Release 5.1 (StatSoft 1997). Mean values ± SD of the more important variables are presented.

We tested three different causal models to investigate which are the causes of changes in RGR, using the d-sep test developed by Shipley (2000b, 2004; DGRAPH at http://callisto.si.usherb.ca:8080/bshipley/book.htm). The variable "time" used in these models was calculated for each harvest as the mean number of days within the growth interval. Data were ln-transformed before the analysis.

Plasticity index was calculated for RGR, NAR, LAR, SLA and LMR, for each species as the ratio: (maximum value − minimum value)/(maximum value), using the values of the four periods (Valladares et al., 2000). Differences in plasticity index between these growth variables were tested using the Mann–Whitney *U* test (also with the Statistica program).

Results

Growth during a two-months period

Considering the total growth period of 62 days, RGR values varied from 91 mg g^{-1} day^{-1} for the fast-growing *Ae. longissima* Schweinf. and Muschl. to 68 mg g^{-1} day^{-1} for the slow-growing *Ae. comosa* Sm. in Sibth. and Sm. var *comosa*; in comparison, the cultivated wheat (*T. aestivum* L.) also grew fast, at a rate of 85 mg g^{-1} day^{-1} (Appendix 1).

RGR values for all the studied species were positively correlated with their LAR values ($r = 0.76$, $P < 0.001$, Figure 2a), but not with NAR values ($r = -0.002$; $P = 0.99$, Figure 2b). The differences in LAR between species were mostly explained (82% variance) by the SLA variation ($r = 0.91$, $P < 0.001$), and marginally (13%) by LMR variation ($r = 0.36$, $P = 0.10$). Consequently, the differences in RGR between species were positively correlated with the variation in SLA ($r = 0.69$; $P < 0.01$; Figure 2c). NAR values were negatively correlated with LAR ($r = -0.55$; $P < 0.01$), due to the negative correlation between NAR and SLA ($r = -0.50$; $P < 0.05$).

The proportion of biomass allocated to roots (RMR) was negatively correlated with leaf biomass allocation (LMR, $r = -0.52$; $P < 0.05$), as well as with stem biomass allocation (SMR, $r = -0.53$; $P < 0.05$). RGR showed a nearly significant negative correlation with the biomass allocation to roots (RMR, $r = -0.38$; $P = 0.08$, Figure 2d).

The RGR for the two-months growth period was positively correlated with leaf N concentration ($r = 0.44$, $P < 0.05$; Figure 2e). This chemical variable (leaf N concentration) was positively correlated with the morphological variable LAR ($r = 0.49$; $P < 0.05$); dissecting the LAR components, leaf N concentration was positive correlated with plant allocation to leaves (LMR, $r = 0.47$; $P < 0.05$; Figure 2f), but did not show a significant correlation with leaf structure (SLA, $r = 0.34$; $P = 0.12$).

The values of growth rate components (GRC) were 1.01 for LAR and only 0.04 for NAR; within the LAR, the growth rate components were 0.84 for SLA and 0.13 for LMR.

Growth during each of two-weeks periods

Comparing the RGR values for all the species and for the four growth periods considered, the maximum RGR value was shown by *Ae. longissima* during the first period (146 mg g^{-1} day^{-1}), whereas the minimum was shown by *Ae. geniculata* Roth during the last period (47 mg g^{-1} day^{-1}). (Appendix 2).

The variables more closely associated with RGR differences between species, for each two-weeks period, differed with those observed for the two-months period. The main difference was that RGR values were positively correlated with NAR for each of the two weeks periods (Figures 3b, d, f and h), in contrast with the non-significant correlation observed for the total growth period (Figure 2b). Another striking difference was that RGR values were not significantly correlated with either LAR or SLA during the 2nd, 3rd and 4th periods (Figures 3c, e and g), in contrast with the strong positive correlation found when the two-months growth period was considered (Figure 2a and 2c).

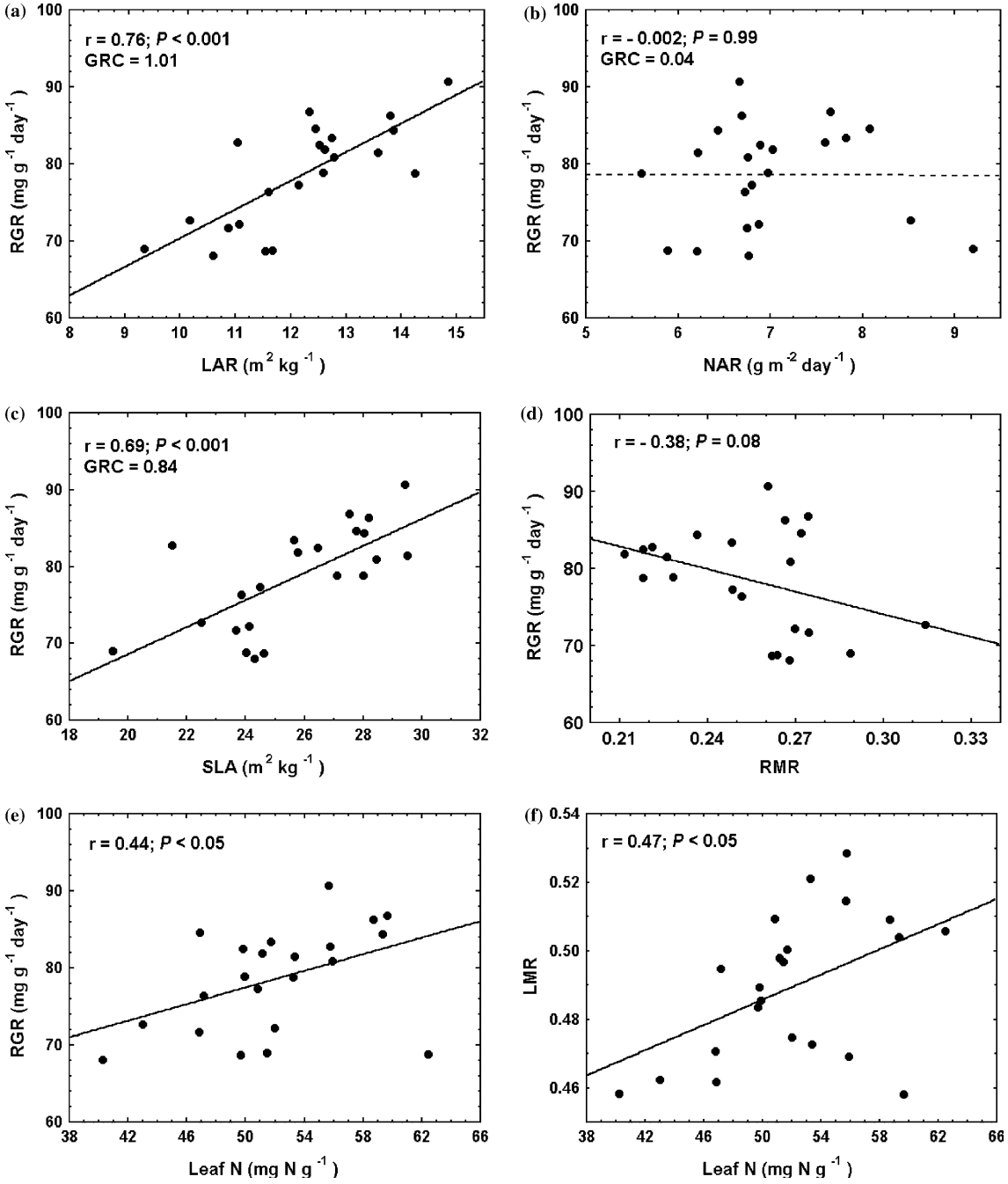

Figure 2. Relationships between relative growth rate (RGR) and five growth variables: (a) leaf area ratio (LAR), (b) net assimilation rate (NAR), (c) specific leaf area (SLA), (d) root mass ratio (RMR), and (e) leaf N concentration. Relationship between leaf mass ratio (LMR) and leaf N concentration (f). Values for all variables are the mean values for the 62 days of the growing period, except those of leaf N concentration (leaves taken at day 62 ± 5.6). Values of growth rate components (GRC) are inserted in Figures 2a, 2b and 2c. Solid and dashed regression lines indicate a significant or non-significant relationship, respectively.

GRC calculated for each of the two-week periods were always higher for NAR (from 0.76 to 1.23) than for LAR (from 0.35 to −0.05) (Figure 3). It is also remarkable that GRCs for NAR increased with time, whereas GRCs for LAR decreased (Figure 3, notice that in this figure the

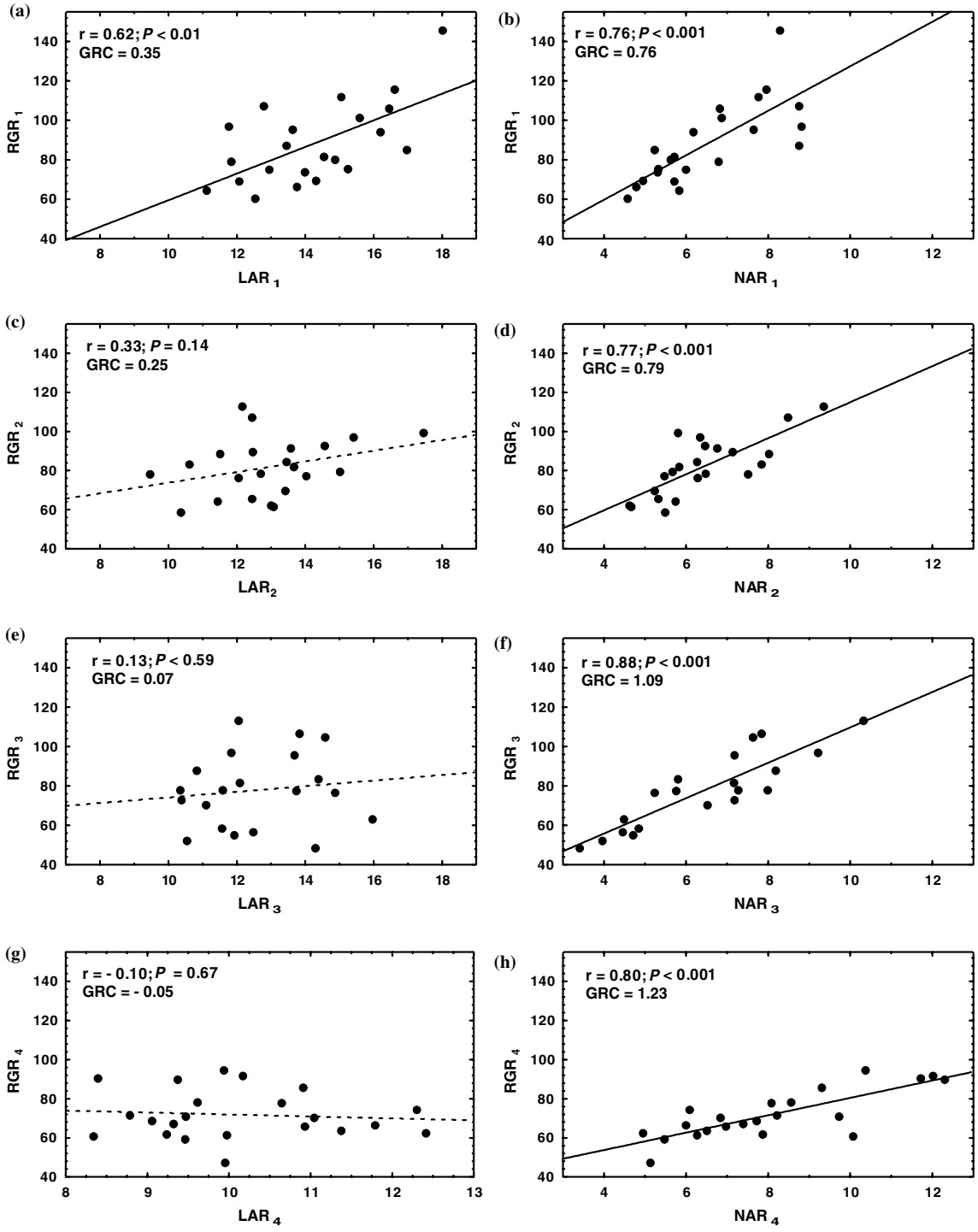

Figure 3. Relationships between relative growth rate (RGR) and two growth variables: leaf area ratio (LAR) and net assimilation rate (NAR), for the first (a–b), second (c–d), third (e–f) and fourth (g–h) growth periods of about 13–19 days each. Units for RGR are mg g^{-1} day^{-1}, for LAR m^2 kg^{-1} and for NAR g m^{-2} day^{-1}. Values of growth rate components (GRC) are inserted in the graph. Solid and dashed regression lines indicate a significant or non-significant relationship, respectively.

RGR is the dependent variable, whereas for the calculations of GRC, the RGR is the independent variable; see Material and methods). In addition, GRC of NAR for each growth period was positively correlated with the average mean daily photon flux density during the same growth period ($r = 0.95$; $P < 0.05$).

Temporal variations in RGR and their components

The all-species mean value for RGR decreased with time: from 88 ± 21 (period 1), to 82 ± 15 (period 2), to 78 ± 19 (period 3) and lastly to 72 ± 12 mg g^{-1} day^{-1} for the 4th period. Despite this general trend of slower RGR with time, there were great differences between species in the change in RGR with time. For example, comparing the 1st and the 4th growth periods, the RGR of *Ae. longissima* decreased from 146 to 78 mg g^{-1} day^{-1} (68 mg g^{-1} day^{-1} decrease), whereas RGR of *Ae. comosa* var. *comosa* increased from 60 to 91 mg g^{-1} day^{-1} (31 mg g^{-1} day^{-1} increase). The result is that the growth patterns between species varied from a short time interval (two weeks) to the next. Thus, RGR between periods were not significantly correlated (r ranging from −0.27 to 0.17; $P > 0.20$).

The variation of NAR between species was also very dynamic with time. The extreme case was illustrated by the nearly significant negative correlation between NAR values for period 1 vs. 3 ($r = -0.41$; $P = 0.07$); that is, some species with higher NAR during the first 2-week period had the lower NAR one month later (3rd period). In general, there was no significant correlation in the NAR values between the four growth periods studied (r ranging from −0.32 to 0.17; $P > 0.15$), with the exception mentioned above (period 1st vs. 3rd; which was negative).

In contrast, the ranking of species for morphological variables was more stable. LAR values were significantly and positively correlated between almost all two-week growth periods (r from 0.38 to 0.79; $P < 0.05$); with the exception of period 1 vs. 4, when the correlation was also positive ($r = 0.30$; $P = 0.18$). SLA for all species were also significantly correlated between the four growth periods, by all possible pairs (r from 0.43 to 0.86; $P < 0.05$); with the exception of period 2 vs. 4, for which the correlation was also positive ($r = 0.28$; $P = 0.20$).

Mean plasticity index of NAR, for all species, was significantly higher (0.40 ± 0.15) than the mean of LAR plasticity (0.30 ± 0.08); as consequence of the very low plasticity of leaf biomass allocation, LMR (0.19 ± 0.05) (Figure 4).

Which trait accounted for most of the temporal changes in RGR? The analyses of temporal differences in relative growth rates ($RGR_4 - RGR_1$) for all species showed a positive significant correlation with their temporal differences in NAR ($NAR_4 - NAR_1$, $r = 0.72$, $P < 0.001$; Figure 5a). However, RGR changes in time did not correlate significantly with temporal changes on LAR ($LAR_4 - LAR_1$, $r = 0.22$; $P = 0.33$; Figure 5b).

Three different causal models were tested to investigate which are the causes of changes in RGR (by using the d-sep test; Shipley, 2000b, 2004) (Figure 6). Model A assumes a decrease of SLA with time and that SLA has a negative effect on NAR. Other assumptions are that SLA determines LAR (being LAR = SLA × LMR), and that both LAR and NAR determine RGR. Model B is similar to A but we have added the assumption that LMR affects LAR. In the model C we have added a new causal effect, that there is a change in LMR with the time; we have also assumed that NAR is negatively affected by LAR, instead of by SLA, like in models A and B.

Model A is rejected by the data ($P = 0.00002$; Table 1). Looking at the individual claims of

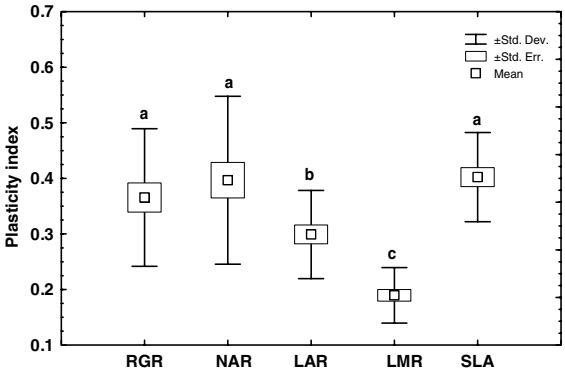

Figure 4. Mean plasticity index for RGR, NAR, LAR, LMR and SLA, for the 22 species studied. Plasticity index was calculated for each species as the ratio: (maximum value – minimum value)/ (maximum value) for the four periods. Different letters mean significant differences ($P < 0.05$; Mann–Whitney U test).

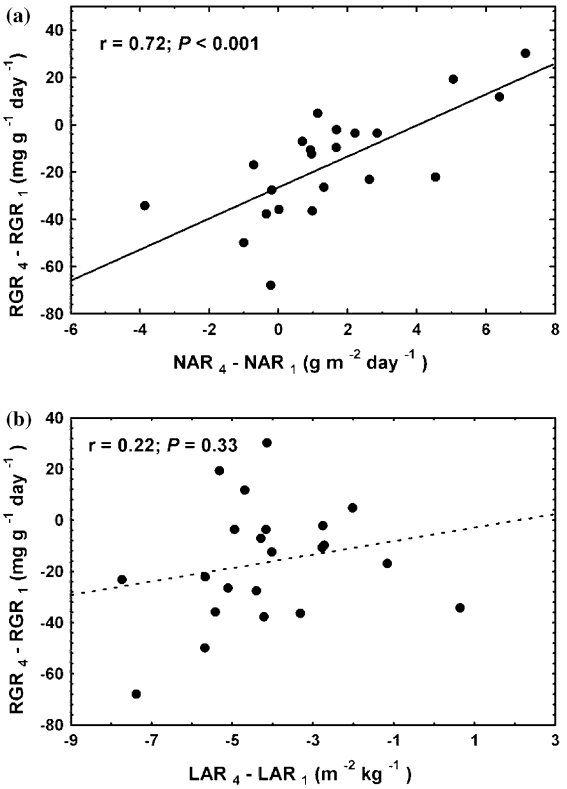

Figure 5. Relationship between the temporal variation in relative growth rate (RGR_4–RGR_1) and the change in: (a) net assimilation rate (NAR_4–NAR_1), and (b) leaf area ratio (LAR_4–LAR_1). RGR_1, LAR_1 and NAR_1 are the values for the first growth period, and RGR_4, LAR_4 and NAR_4 are the values for the last growth period. Solid and dashed regression lines indicate a significant or non-significant relationship, respectively.

conditional independence implied by this model (Table 1), we can observe that two of them are wrong: NAR and Time are not independent conditional on SLA, and LAR and Time are not independent conditional on SLA. Model B is also rejected ($P < 10^{-6}$), three claims of conditional independence are wrong: one of them (NAR and Time on SLA) was already mentioned in model A, besides NAR and LMR are not independent conditional on SLA, and LMR and Time are not independent. In contrast, model C was not rejected by the data, and the probability of a causal process hypothesized by this model was 0.621 (Table 1). The causal relationships proposed by this model are that the plant age (Time) causes a decrease in SLA, and an increase in the leaf biomass allocation (LMR). Both variables – SLA and LMR – determine LAR (as it is the product of them). On the other hand, an increase in LAR causes a decrease in NAR, but there is not any effect of the plant age (Time) on the changes in NAR. Changes in both variables – NAR and LAR – are causes of changes in RGR (See Figure 6).

Discussion

A novel contribution of this growth analysis study is that it covers a wide range of congeneric species (20 out of the known 22 *Aegilops* species). Using congeneric species has advantages and disadvantages. A possible disadvantage is that the obtained results can be unique to this group, and thus could not be general for other groups of species; although improbable, it should be contrasted. The main advantage of using related species is that they share common features and then,

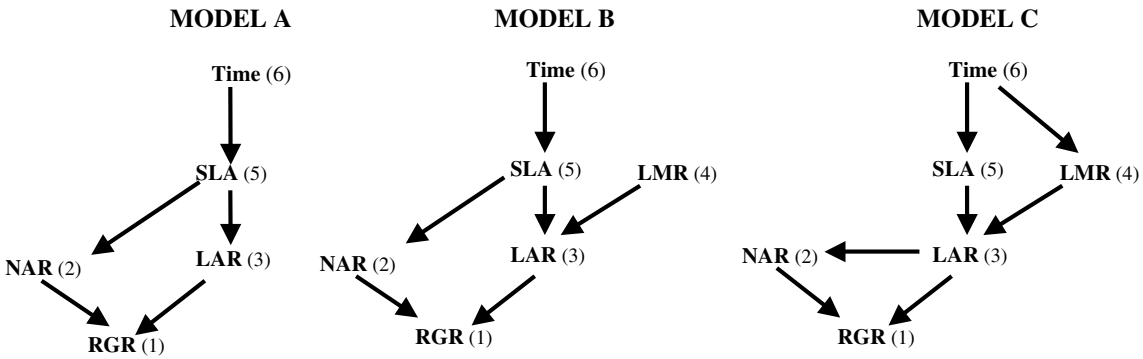

Figure 6. Three alternative hypotheses (models A, B and C) describing the causal-effect relationships among growth variables. Numbers indicate the variable number, which is used in Table 1. Abbreviations as in Figure 2. The model C was not rejected by the data (16 df, value of the Fisher's C statistics = 13.7; $P = 0.621$) using the d-sep test developed by Shipley (2002b, 2004).

Table 1. Basic set for the partial independence constraints implied by each of the three models shown in Figure 6. The notation "(X,Y){A, B, ...}" means that variables X and Y are d-separated, and hypothesised to be probabilistically independent, conditional on the set of variables {A, B, ...} and the "Φ" represents the null (empty) set. Pearson's partial correlation coefficient (r), and probability assuming the null hypothesis (in parentheses), are given for each conditional independence claim; values in bold have a probability below 0.05. The overall model is tested with Fisher's C statistic, values in bold means that the model is rejected by the data

Model A		Model B		Model C	
Basic set	r (probability)	Basic set	r (probability)	Basic set	r (probability)
(1,5){2,3,6}	−0.011 (0.919)	(1,4){2,3}	−0.042 0.708)	(1,4){2,3,6}	0.094 (0.401)
(1,6){2,3}	−0.136 (0.216)	(1,5){2,3, 6}	−0.011 (0.919)	(1,5){2,3, 6}	−0.011 (0.919)
(2,3){5}	−0.213 (0.05)	(1,6){2,3}	−0.136 (0.217)	(1,6){2,3}	−0.136 (0.217)
(2,6){5}	**−0.229** (0.034)	(2,3){4,5}	0.160 (0.147)	(2,4){3,6}	0.039 (0.729)
(3,6){5}	**0.457** (0.0000)	(2,4){5}	**−0.251** (0.020)	(2,5){3,6}	−0.089 (0.423)
		(2,6){5}	**−0.229** (0.034)	(2,6){3}	−0.130 (0.238)
		(3,6){4,5}	0.013 (0.907)	(3,6){4,5}	0.013 (0.907)
		(4,5){6}	−0.141 (0.199)	(4,5){6}	−0.141 (0.199)
		(4,6){Φ}	**0.749** (10^{-6})		
10 df, C = **39.48** (0.00002)		18 df, C = **108.99** ($< 10^{-6}$)		16 df, C = 13.7 (0.621)	

there is not noise for including data from different groups (as happens in many comparative studies about RGR, including dicots and monocots, erect vs. prostrate, annuals and perennials, etc.).

The other novelty of this study is that this large group of species has been grown under common field conditions. Most of the recent growth studies have been carried out under controlled conditions, in growth chambers or glasshouses with constant environmental conditions; their aims were to compare RGR of different species or RGR of plants subjected to different treatments. In comparison, plants under field conditions usually perceive limiting or sub-optimum levels of resources (e.g., water and nutrients), or supra-optimum levels (e.g., of light and temperature); in addition, environmental variables are very heterogeneous in space and time (Garnier and Freijsen, 1994; see Figure 1). As stated in the introduction, both approaches are valid and complementary, providing each of them important information about plant growth. Lab experiments (environmental controlled experiments) have the advantages of repeatability, easy monitoring and controlling environmental parameters, easy access to roots, easy possibility of changing environmental parameters, constant conditions along time, etc.. In contrast, field experiments are more realistic, and the environmental conditions are within natural levels (for example light levels in lab experiments are in general very low and far below natural habitat levels; Garnier and Freijsen, 1994). In a survey in Science Citation Index (for all the references up to August 2004), the search for plant RGR studies resulted in only ca. 18 % carried out under field conditions, and only very few of them made comparative studies with several species. Therefore, there is a considerable gap in RGR studies under field conditions, which makes difficult to conclude generalisations.

In general, RGR values measured under field conditions are much lower than those attained by the same species in controlled experiments under more favourable growing conditions (Garnier and Freijsen, 1994). Thus, mean RGR for all *Aegilops* species grown in the field was 78 ± 7 mg g^{-1} day^{-1}; whereas the same species cultivated in growth chambers reached about double these values (154 ± 18 mg g^{-1} day^{-1}, comparing individuals with similar mass; Villar et al., 1998). In a comparative review, Garnier and Freijsen (1994) found that field-grown plants had up to five times lower RGR values than equivalent plants grown in laboratory conditions.

The contrasting growing conditions will affect both the RGR values and the relative contribution of LAR, NAR and SLA to the resulting RGR. As explained before, temperature or light may change

the relative contribution of SLA or NAR to RGR (see Loveys et al., 2002; Shipley, 2002).

Under field conditions, there are many interacting factors, such as light, temperature, soil moisture and nutrients, and these vary with time (e.g., Figure 1) which makes it difficult to predict their effects on growth rates. Most experiments designed to investigate the effects of environment on growth rates have used mainly two approaches: (1) the factorial experiment, where plants are grown with different levels (treatments) of one or more factors, such as light or mineral nutrients, or (2) to subject plants to a quick change in a certain factor, and then maintain the new environment during the rest of the experiment. For example, Shipley (2000a) studied growth patterns of plants subjected to an irradiance switch (from 550 to 100 μmol m^{-2} s^{-1}), and found instantaneous changes in NAR and SLA after a few hours, while LMR did not vary. These experiments with temporal changes in environmental factors have allowed establishing a rank of plasticity (response to changes) in growth features: NAR and RGR are more plastic than SLA, and this more than LMR (Shipley, 2000a). Our study also support these results (Figure 4), although we found that SLA was also highly plastic. In this study when the total vegetative growth period (62 days) was considered, RGR was mostly explained by the variation in plant morphology (LAR), and in particular in leaf structure (SLA). This finding is in agreement with many other studies supporting SLA as a major factor associated with variation in RGR (e.g., Atkin et al., 1996; Cornelissen et al., 1996; Garnier, 1992; Lambers et al., 1998; Marañón and Grubb, 1993; Poorter and Remkes, 1990; Poorter and Van der Werf, 1998; Van den Boogaard et al., 1996).

The biomass allocation to roots also explained (negatively) the differences in RGR between *Aegilops* species; that is, those species growing faster under field conditions allocated less biomass to roots. In the experiment with the same species, but growing under controlled laboratory conditions, RGR values were also significantly and negatively correlated with RMR (Villar et al., 1998). In that study, the inherent variation in RMR was found to be negatively correlated with the annual rainfall in the native habitat of the species. That is, *Aegilops* species from moister habitats seemed to allocate less to roots, and grow faster, while species from dry habitats tended to invest more in roots, and grow slower. In this common field experiment the species RMR values were not correlated with the annual rainfall in their native habitats ($r = -0.23$, $P = 0.50$). However, RMR values obtained in the field were positively correlated with RMR values of the same species measured in the laboratory ($r = 0.46$, $P < 0.05$), which might suggest that root allocation (RMR) is a variable with a low degree of plasticity, and could have an adaptive role in *Aegilops* species.

Relative growth rate was also significantly and positively correlated with the leaf N concentration. Nitrogen is an essential component of proteins, and thus contributes to metabolic rates, and consequently to growth rates (see Poorter and Bergkotte, 1992; De Groot et al., 2003). LAR and LMR were also correlated positively with N concentration. However, in a recent review (Wright and Westoby, 2001) it was argued that RGR is, in general, negatively correlated with N concentration in leaves.

In contrast, the growth analysis of field-grown *Aegilops* species, considering short-time intervals (13–19 days), gave strikingly different results compared with the total growth period (62 days). At short-time scale (weeks), RGR was best explained by NAR (that occurred for all the four periods, and always with high r values), but RGR did not show a significant correlation with LAR during the 2nd, 3rd and 4th periods. Moreover, the relative importance of NAR increased with time which is reflected by the increasing GRC values from 0.76 to 1.23; in contrast, the contribution of LAR decreased (GRC values) from 0.35 to −0.05 (Figure 3). This increase of importance of NAR with time could be partly due to the increased daily photon flux density with time; in fact there was a positive correlation between GRC of NAR and the mean daily photon flux density. Shipley (2002) argued that in studies with a daily photon flux density higher than 20 mol m^{-2}, RGR was better explained by NAR. At the latitude of this field study (37° N), that level of irradiance was reached, and it increased with time (Figure 1a, see Garnier and Freijsen, 1994).

Why are the RGRs best correlated with morphological variables (SLA and LAR) for longer

time periods (months), while they switch to be correlated with physiological variables (NAR) at shorter-time (weeks) scale? The temporal change in RGR along the vegetative stage studied was different between species, most probably because they responded differently to the changing field conditions (e.g., light, temperature and soil moisture). Thus, the RGRs estimated at different time periods were not correlated; that is, the species growing fastest in one growth period was not in other growth periods. The temporal change in NAR also differed between species; that is, there was no significant correlation between NAR measured at different growth periods. NAR is related to the net carbon balance, predominantly including the physiological processes of photosynthesis and respiration (Lambers et al., 1998). The ability of these physiological functions to respond to rapid changes in environmental conditions (like in this field study) must be faster than that of the morphological features; this is supported by the higher plasticity index of NAR compared with that of LAR (Figure 4). Consequently, it is expected that these short-time responses in NAR will better explain the attained, short-time variation in RGR. In fact, the variability over time in RGR (e.g., its standard deviation) of each species was positively correlated to the variability of NAR ($r = 0.42$; $P < 0.05$), but not with LAR, SLA or LMR ($P > 0.15$).

In contrast with NAR, the morphological plant traits, LAR and SLA, showed a between-species pattern relatively stable during the growth period; that is, species with higher LAR at the beginning of the experiment, maintained that differential morphological feature during the whole period (two months). This would explain why the RGR for the whole growth period (62 days) was better correlated with LAR and SLA, than that for NAR.

The model C tested and not rejected by our data ($P = 0.621$; Figure 6), can help to explain the causal relationships determining the observed changes in RGR. It has been generally found an ontogenetic decrease of SLA, as the leaves get older (Hunt, 2003; Poorter and Pothmann, 1992). However, changes in LMR with ontogeny are not so general in the literature. Some studies have documented a decrease in LMR but others showed no change or even an increase in LMR (e.g., Hunt, 1990; Poorter and Pothman, 1992), as found here. Because SLA has more importance in determining LAR than LMR (see Results and Figure 2c), there is a decrease in LAR with time. It has been found also that LAR is in general negatively associated with NAR (Konings, 1989; Poorter and Remkes, 1990). Changes in RGR are due to changes in NAR and LAR. Importantly, NAR is not affected by the variable time (according to the model), as it happens with the components of LAR (SLA and LMR). That does not mean that NAR is stable with time. NAR showed a great temporal variability, but there was no significant pattern with time.

Are these results comparable with those under laboratory conditions? In general, when plants are cultivated in controlled conditions, the temporal changes in RGR tend to be consistent between species (e.g., for the same 20 *Aegilops* species in Villar et al., 1998; for seedlings of 16 woody species in Antúnez et al., 2001). The homogeneous conditions of light, temperature and water availability during the laboratory experiments can explain the correlation in RGR between periods, as well as in LAR, SLA and NAR. Also, in laboratory experiments, the variation in the physiological growth component (NAR) tends to be smaller than that in the morphological component (LAR); e.g., for a set of 24 species Poorter and Remkes (1990) found a coefficient of variation of 15% for NAR and 29% for LAR. This higher range of variation in LAR could also explain its greater contribution to differences in RGR between species in laboratory experiments.

The general trend of the *Aegilops* species' growth rates was to decline with time, although there were some species showing different trends (maintained or increased RGR). This reduction in growth rate with plant age has been well documented, and explained by ontogenetic changes, higher allocation to low-efficiency tissues, and self-shading (e.g., Hunt, 2003; Poorter and Pothmann, 1992; Romero and Marañón, 1994; Shipley, 2000a). However, there are experiments showing that RGR values increase with time or have complex patterns for certain periods (Antúnez et al., 2001; Higgs and James, 1969; Van Andel and Jager, 1981).

In this study of field-grown *Aegilops* species, the temporal changes in RGR were mostly

explained by the temporal changes of NAR, rather than by the temporal changes in LAR. In other experiments, the temporal changes in RGR have also been associated with variation in NAR (Antúnez et al., 2001).

The importance of NAR in determining the growth patterns on field conditions is therefore supported by two lines of evidence: (1) it is the major factor contributing to the species' RGR in the short term (weeks); and (2) it is significantly correlated with the temporal changes in RGR.

In summary, most of the plant growth studies have been made in controlled, uniform conditions, and have emphasised the major contribution of plant morphological traits, namely LAR and SLA, in determining RGR. In the laboratory environment, the conditions of temperature, irradiance, moisture and nutrients are constant, or with uniform, periodic changes. In these artificial conditions, it would be expected that the morphological and structural features (such as LAR and SLA) are more relevant for plant growth, than the physiological functions (such as photosynthesis and respiration), which are more plastic and dependent of environmental conditions. However, under field conditions and considering short-time periods (e.g., days or weeks), the differences in RGR amongst species seem to be explained by highly dynamic variables, such as NAR. When a longer period is considered (e.g., months) the fluctuations of resources and conditions, characteristic of field environment, can minimise the importance of NAR, and instead their more stable and species-characteristic, morphological features (LAR and SLA) become more relevant for the species' growth pattern.

Acknowledgements

We thank Roderick Hunt and Bill Shipley for their helpful comments to a previous version of the manuscript; to Michiel Van Slageren (ICARDA) for providing information about the *Aegilops* and *Amblyopyrum* species; to John Peacock (ICARDA) for providing the seeds and to Enrique Fernández for providing meteorological data. This research was supported by a Post-Doctoral Fellowship (Dirección General de Investigación Científica y Técnica, Spain) to RV, and by Project PB98- 1031 (Dirección General de Investigación Científica y Técnica, Spain).

Appendix 1. List of the 22 species studied (20 *Aegilops*, 1 *Amblyopyrum* and *Triticum aestivum*, cv. Yecora), number of the collection code at the International Center for Agricultural Research in the Dry Areas (ICARDA, Aleppo, Syria) and mean values of different plant variables: Initial M (initial dry mass at day 0); RGR (relative growth rate); NAR (net assimilation rate); LAR (leaf area ratio); SLA (specific leaf area); LMR (leaf mass ratio); SMR (stem mass ratio) and RMR (root mass ratio). Nomenclature is according to Van Slageren (1994). Values of all variables, except Initial M are the mean values for the whole vegetative growth period (62 days).

Code	Species	Initial M (mg)	RGR (mg g^{-1} day^{-1})	NAR (g m^{-2} day^{-1})	LAR (m^2 kg^{-1})	SLA (m^2 kg^{-1})	LMR	SMR	RMR
400736	*Ae. biuncialis* Vis.	24.5	81.90	7.02	12.61	25.78	0.498	0.289	0.212
401094	*Ae. caudata* L.	20.0	78.86	6.97	12.59	27.10	0.486	0.288	0.228
401508	*Ae. columnaris* Zhuk.	29.1	68.73	6.21	11.54	24.63	0.483	0.249	0.262
400582	*Ae. comosa* Sm. in Sibth. and Sm. var *comosa*	31.8	68.08	6.76	10.60	24.32	0.458	0.276	0.268
400715	*Ae. crassa* Boiss.	36.2	72.76	8.52	10.17	22.50	0.462	0.236	0.314
401320	*Ae. cylindrical* Host	17.8	82.51	6.89	12.51	26.45	0.489	0.288	0.218
401007	*Ae. geniculata* Roth	36.0	71.76	6.75	10.87	23.66	0.471	0.252	0.274
401483	*Ae. juvenalis* (Thell.) Eig	38.7	77.36	6.80	12.15	24.50	0.510	0.245	0.249
400885	*Ae. kotschyi* Boiss.	26.1	83.45	7.82	12.74	25.63	0.500	0.248	0.248
400531	*Ae. longissima* Schweinf. and Muschl.	11.8	90.67	6.66	14.85	29.44	0.515	0.228	0.260
401105	*Ae. neglecta* Req. ex Bertol.	24.5	68.83	5.89	11.66	24.01	0.506	0.229	0.264

Appendix 1. Continued.

Code	Species	Initial M (mg)	RGR (mg g^{-1} day^{-1})	NAR (g m^{-2} day^{-1})	LAR (m^2 kg^{-1})	SLA (m^2 kg^{-1})	LMR	SMR	RMR
401290	*Ae. peregrina* (Hack. in J. Fraser) Maire and Weiller	23.3	78.83	5.60	14.25	28.00	0.521	0.255	0.218
400902	*Ae. searsii* Feldman and Kislev ex Hammer	23.5	69.05	9.20	9.36	19.47	0.497	0.231	0.289
400725	*Ae. speltoides* Tausch var. *speltoides*	18.9	86.34	6.69	13.80	28.19	0.509	0.232	0.266
400649	*Ae. tauschii* Coss.	28.2	81.51	6.22	13.57	29.51	0.473	0.303	0.226
401501	*Ae. triuncialis* L.	24.5	76.38	6.72	11.60	23.87	0.495	0.250	0.252
400017	*Ae. umbellulata* Zhuk.	29.8	72.23	6.88	11.06	24.12	0.475	0.256	0.270
400547	*Ae. uniaristata* Vis.	17.4	80.94	6.75	12.77	28.45	0.469	0.265	0.268
401842	*Ae. vavilovii* (Zhuk.) Chennav.	20.8	82.81	7.59	11.04	21.51	0.528	0.246	0.221
401446	*Ae. ventricosa* Tausch	20.9	84.42	6.43	13.85	28.04	0.504	0.259	0.236
400274	*Amblyopyrum muticum* (Boiss.) Eig	25.1	86.84	7.65	12.33	27.52	0.458	0.272	0.274
	Triticum aestivum L. cv. *Yecora*	53.5	84.63	8.08	12.44	27.78	0.462	0.269	0.272

Appendix 2. Mean values of different plant variables for the four growth periods (indicated by subscripts): RGR (relative growth rate; mg g^{-1} day^{-1}); NAR (net assimilation rate; mg g^{-2} day^{-1}); LAR (leaf area ratio; m^2 kg^{-1}); LMR (leaf mass ratio) and SLA (specific leaf area; m^2 kg^{-1}). Code is the number of the collection code at the International Center for Agricultural Research in the Dry Areas (ICARDA, Aleppo, Syria). Nomenclature is according to Van Slageren (1994).

Code	Species	RGR_1	NAR_1	LAR_1	LMR_1	SLA_1	RGR_2	NAR_2	LAR_2	LMR_2	SLA_2	RGR_3	NAR_3	LAR_3	LMR_3	SLA_3	RGR_4	NAR_4	LAR_4	LMR_4	SLA_4
400736	*Ae. biuncialis*	75.2	5.3	15.2	0.47	32.3	107.1	8.5	12.4	0.49	25.7	55.0	4.7	11.9	0.52	23.2	94.5	10.4	9.9	0.51	19.7
401094	*Ae. caudata*	84.9	5.2	17.0	0.46	37.2	81.9	5.8	13.7	0.44	31.8	96.9	9.2	11.8	0.51	24.7	61.8	7.9	9.2	6.54	17.7
401508	*Ae. columnaris*	69.2	5.7	12.1	0.40	30.0	61.3	4.7	13.1	0.47	27.2	77.8	7.3	11.6	0.53	22.2	67.1	7.4	9.3	0.55	17.0
400582	*Ae. comosa*	60.3	4.6	12.5	0.41	31.5	64.4	5.7	11.4	0.42	27.8	52.2	4.0	10.5	0.48	23.0	90.6	11.7	8.4	0.52	16.7
400715	*Ae. crassa*	107.3	8.7	12.8	0.45	29.7	58.6	5.5	10.4	0.45	24.0	na	na	na	na	na	70.9	9.7	9.5	0.48	20.1
401320	*Ae. cylindrical*	73.9	5.3	14.0	0.44	32.6	84.4	6.3	13.4	0.48	28.6	113.0	10.3	12.0	0.52	23.8	61.6	6.3	10.0	0.55	18.5
401007	*Ae. geniculata*	64.3	5.8	11.1	0.42	27.2	88.5	8.0	11.5	0.51	23.2	87.8	8.2	10.8	0.49	22.5	47.4	5.1	9.9	0.48	20.8
401483	*Ae. juvenalis*	81.7	5.7	14.6	0.45	32.0	69.6	5.2	13.4	0.48	28.0	81.7	7.2	12.1	0.55	22.6	78.1	8.6	9.6	0.54	18.1
400885	*Ae. kotschyi*	111.9	7.8	15.0	0.46	32.7	77.2	5.5	14.0	0.49	28.7	48.6	3.4	14.3	0.56	26.1	89.8	12.3	9.4	0.50	18.2
400531	*Ae. longissima*	145.7	8.3	18.0	0.46	39.7	99.2	5.8	17.4	0.51	35.0	63.3	4.5	16.0	0.57	28.5	77.7	8.1	10.6	0.50	21.1
401105	*Ae. neglecta*	66.4	4.8	13.8	0.45	30.9	78.3	6.5	12.7	0.47	27.5	73.0	7.2	10.4	0.53	19.9	59.3	5.5	9.5	0.58	16.6
401290	*Ae. peregrina*	69.5	4.9	14.3	0.45	31.7	97.0	6.3	15.4	0.52	29.7	76.6	5.2	14.9	0.57	26.7	74.3	6.1	12.3	0.56	22.4
400902	*Ae. searsii*	87.2	8.7	13.4	0.45	29.3	78.1	7.5	9.5	0.46	21.2	na	na	na	na	na	60.7	10.1	8.3	0.52	16.4
400725	Ae. speltoides var. *speltoides*	106.0	6.8	16.5	0.45	37.5	79.5	5.7	15.0	0.46	32.9	104.8	7.6	14.6	0.54	27.5	70.2	6.8	11.0	0.56	20.3
400649	*Ae. tauschii*	94.0	6.2	16.2	0.42	38.6	91.3	6.8	13.6	0.43	32.1	77.7	5.8	13.7	0.51	27.4	66.5	6.0	11.8	0.53	22.3
401501	*Ae. triuncialis*	96.8	8.8	11.8	0.43	27.2	83.2	7.8	10.6	0.47	22.8	58.5	4.8	11.6	0.54	21.9	62.5	4.9	12.4	0.56	22.7
400017	*Ae. umbellulata*	75.2	6.0	12.9	0.43	29.9	65.6	5.3	12.4	0.44	28.8	77.7	8.0	10.3	0.51	21.2	71.7	8.2	8.8	0.52	17.2
400547	*Ae. uniaristata*	115.7	8.0	16.6	0.42	39.1	89.4	7.1	12.5	0.42	30.9	56.7	4.4	12.5	0.50	26.0	65.8	7.0	10.9	0.53	21.2
401842	*Ae. vavilovii*	79.2	6.8	11.8	0.46	25.9	112.9	9.4	12.2	0.52	23.7	70.5	6.5	11.1	0.58	19.4	68.6	7.7	9.1	0.57	16.2
401446	*Ae. ventricosa*	101.4	6.9	15.6	0.45	35.1	92.6	6.5	14.6	0.50	29.7	83.5	5.8	14.4	0.54	26.9	63.7	6.5	11.4	0.5	21.6
400274	*Amblyopyrum muticum*	95.4	7.6	13.6	0.40	34.0	76.4	6.3	12.1	0.43	28.6	95.7	7.2	13.7	0.49	28.4	85.7	9.3	10.9	0.49	22.5
	Triticum aestivum cv. Yecora	80.1	5.6	14.9	0.38	39.3	62.1	4.6	13.0	0.46	29.6	106.5	7.8	13.8	0.54	26.3	91.8	12.0	10.2	0.45	22.2

na: not available.

References

Antúnez I, Retamosa E C and Villar R 2001 Relative growth rate in phylogenetically related deciduous and evergreen woody species. Oecologia 128, 172–180.

Atkin O K, Botman B and Lambers H 1996 The causes of inherently slow growth in alpine plants: An analysis based on the underlying carbon economies of alpine and lowland *Poa* species. Funct. Ecol. 10, 698–707.

Cakmak I, Cakmak O, Eker S, Ozdemir A, Watanabe N and Braun H J 1999 Expression of high zinc efficiency of *Aegilops tauschii and Triticum monococcum* in synthetic hexaploid wheats. Plant Soil 215, 203–209.

Cornelissen J H C, Castro Diez P and Hunt R 1996 Seedling growth allocation and leaf attributes in a wide range of woody plant species and types. J. Ecol. 84, 755–765.

De Groot C C, Marcelis L F M, van den Boogaard R, Kaiser W M and Lambers H 2003 Interaction of nitrogen and phosphorus nutrition in determining growth. Plant Soil 248, 257–268.

García D, Rodríguez J, Panadero P, Marañón T and Villar R 1997 Tasas de crecimiento en 21 especies de trigo silvestre y su relación con la tasa de fotosíntesis y la concentración de nitrógeno foliar. *In* Nutrición mineral de las plantas en la agricultura sostenible. Eds. R Sarmiento, E O Leidi and A Troncoso. pp. 83–90. Junta de Andalucía Consejería de Agricultura y Pesca, Sevilla.

Garnier E 1992 Growth analysis of congeneric annual and perennial grass species. J. Ecol. 80, 665–675.

Garnier E and Freijsen A H J 1994 On ecological inference from laboratory experiments conducted under optimum conditions. *In* A Whole Perspective on Carbon-Nitrogen Interactions. Eds. J Roy and E Garnier. pp. 267–292. SPB Academic Publishing, The Hague.

Grime J P and Hunt R 1975 Relative growth-rate: Its range and adaptive significance in a local flora. J. Ecol. 63, 393–422.

Higgs D E B and James D B 1969 Comparative studies on the biology of upland grasses I. Rate of dry matter production and its control in four grass species. J. Ecol. 57, 553–563.

Hoffmann W A and Poorter H 2002 Avoiding bias in calculations of relative growth rate. Ann. Bot. 80, 37–42.

Hunt R 1990 Basic Growth Analysis. Unwin Hyman Ltd, London. 112 pp.

Hunt R 2003 Growth Analysis, Individual Plants. *In* Encyclopaedia of Applied Plant Sciences. Eds. B Thomas, D J Murphy and D Murray. pp 579–588. Academic Press, London.

Hunt R, Causton D R, Shipley B and Askew P 2002 A modern tool for classical plant growth analysis. Ann. Bot. 90, 485–488.

Hunt R and Parson I T 1974 A computer program for deriving growth-functions in plant growth-analysis. J. Appl. Ecol. 11, 297–307.

Konings H 1989 Physiological and morphological differences between plants with a high NAR or a high LAR as related to environmental conditions. *In* Causes and Consequences of Variation in Growth Rate and Productivity of Higher Plants. Eds. H Lambers, M L Cambridge, H Konings and T L Pons. pp. 101–123. SPB Academic Publishing, The Hague.

Lambers H, Chapin F S III and Pons T L 1998 Plant physiological ecology. Springer-Verlag, New York. 540 pp.

Lambers H and Poorter H 1992 Inherent variation in growth rate between higher plants: A search for physiological causes and ecological consequences. Adv. Ecol. Res. 23, 187–261.

Lambers H, Van den Boogaard R, Veneklaas E J and Villar R 1995 Effects of global environmental change on carbon partitioning in vegetative plants of *Triticum aestivum* and closely related *Aegilops* species. Global Change Biol. 1, 397–406.

Loveys B R, Scheurwater I, Pons T L, Fitter A H and Atkin O K 2002 Growth temperature influences the underlying components of relative growth rate: An investigation using inherently fast- and slow- growing plant species. Plant Cell Environ. 25, 975–997.

Marañón T 1989 Variations in seed size and germination in three *Aegilops* species. Seed Sci. Technol. 17, 583–588.

Marañón T and Grubb P J 1993 Physiological basis and ecological significance of the seed size and relative growth rate relationship in Mediterranean annuals. Funct. Ecol. 7, 591–599.

Poorter H and Bergkotte M 1992 Chemical composition of 24 wild species differing in relative growth rate. Plant Cell Environ. 15, 221–229.

Poorter H and Garnier E 1996 Plant growth analysis: An evaluation of experimental design and computational methods. J. Exp. Bot. 47, 1343–1351.

Poorter H and Garnier E 1999 Ecological significance of inherent variation in relative growth rate and its components. *In* Handbook of Functional Plant Ecology. Eds. F Pugnaire and F Valladares. pp. 82–120. Marcel Dekker Inc., New York.

Poorter H and Pothmann P 1992 Growth and carbon economy of a fast- and slow- growing grass species as dependent on ontogeny. New Phytol. 120, 159–166.

Poorter H and Remkes C 1990 Leaf area ratio and net assimilation rate of 24 wild species differing in relative growth rate. Oecologia 83, 553–559.

Poorter H and Van der Werf A 1998 Is inherent variation in RGR determined by LAR at low irradiance and by NAR at high irradiance? A review of herbaceous species. *In* Inherent Variation in Plant Growth Physiological Mechanisms and Ecological Consequences. Eds. H Lambers, H Poorter and M M I van Vuuren. pp. 309–336. Backhuys Publishers, Leiden.

Romero J M and Marañón T 1994 Long-term responses of *Melilotus segetalis* to salinity. I Growth and partitioning. Plant Cell Environ. 17, 1243–1248.

Shipley B 2000a Plasticity in relative growth rate and its components following a change in irradiance. Plant Cell Environ. 23, 1207–1216.

Shipley B 2000b Cause and Correlation in Biology. A User's Guide to Path Analysis, Structural Equations and Causal Inference. Cambridge University Press, Cambridge. 317 pp.

Shipley B 2002 Trade-offs between net assimilation rate and specific leaf area in determining relative growth rate: Relationship with daily irradiance. Funct. Ecol. 16, 682–689.

Shipley B 2004. Analysing the allometry of multiple interacting traits. Perspect. Plant Ecol. 6, 235–241.

Statsoft Inc 1997 Statistica for Windows Release 5.1. Computer Program Manual. Tulsa OK, USA.

Valladares F, Martinez-Ferri E, Balaguer L, Perez-Corona E and Manrique E 2000 Low leaf-level response to light and nutrients in Mediterranean evergreen oaks: A conservative resource-use strategy? New Phytol. 148, 79–91.

Van Andel J and Jager J C 1981 Analysis of growth and nutrition of six plant species of woodland clearings. J. Ecol. 69, 871–882.

Van den Boogaard R, Goubitz S, Veneklaas E and Lambers H 1996 Carbon and nitrogen economy of 4 *Triticum aestivum* cultivars differing in relative growth rate and water use efficiency. Plant Cell Environ. 19, 998–1004.

Van den Boogaard R and Villar R 1998 Variation in growth and water-use efficiency – a comparison of *Aegilops* species and *Triticum aestivum* L. cultivars. *In* Inherent Variation in Plant Growth. Physiological Mechanisms and Ecological Consequences. Eds. H Lambers, H Poorter and M M I van Vuuren. pp. 289–308. Backhuys Publishers, Leiden.

Van Slageren M W 1994 Wild Wheats: A Monograph of *Aegilops* L and *Amblyopyrum* Jaub and Spach Eig Poaceae. Agricultural University Wageningen, The Netherlands. 512 pp.

Villar R, Veneklaas E J, Jordano P and Lambers H 1998 Relative growth rate and biomass allocation in 20 *Aegilops* (Poaceae) species. New Phytol. 140, 425–437.

Wright I J and Westoby M 2001 Understanding seedling growth relationships through specific leaf area and leaf nitrogen concentration: Generalisations across growth forms and growth irradiance. Oecologia 127, 21–29.

Section Editor: T. Kalapos