

# Contribution of growth components on relative, plant, crop and tuber growth rate of nine potato cultivars in southern Italy

Salvatore Ascione<sup>1</sup>, Celestino Ruggiero<sup>2</sup>✍, Cosimo Vitale<sup>3</sup>

<sup>1</sup>Experimental Institute for Tobacco, 84018 Scafati (SA) Italy

<sup>2</sup>Department of Agricultural Engineering and Agronomy, University of Naples Federico II, 80055 Portici (NA) Italy

<sup>3</sup>Department of Economic and Statistical Science, University of Salerno, Italy

**Abstract:** Nine potato cultivars were field-grown to determine relative growth rate (RGR), crop growth rate (CGR) and tuber growth rate (TGR) in order to ascertain which of these parameters, namely leaf area ratio (LAR), specific leaf area (SLA), leaf mass ratio (LMR), leaf area index (LAI) and net assimilation rate (NAR), are most closely correlated with the differences among the cultivars in RGR, CGR and TGR. Nine samplings were carried, for short-cycle, and 11 for long-cycle cultivars, every seven days. The relations between all the indexes considered for all cultivars were analysed with simple linear correlation, separately for weekly data, every four and eight weeks. The data were also subjected to multivariate analysis with the three-stage least squares estimation method. Relations between RGR, CGR and TGR, and LAR, LMR, SLA, LAI and NAR, varied according to the length of the measurement interval and analytical method employed. Based on simple correlation analysis for seven-day periods, RGR, CGR and TGR always proved closely and positively correlated with values of NAR, less so with LAR and LMR, and still less with LAI, and only slightly correlated with SLA. For four-week intervals, correlation with NAR appeared weak and for eight-week intervals even negative, while the relation with LAR and LAI increased. From multivariate analysis it emerged that the predominant factor affecting RGR was LAR which, together with LAI, negatively conditions NAR. Upon CGR and TGR an important role is played by LAI which directly and positively affects CGR and TGR, and negatively NAR. Time always showed a negative effect on NAR and positive on RGR and CGR, while LAR had a negative effect on NAR, CGR and TGR.

In conclusion, for short periods the differences between cultivars in RGR, CGR and TGR appear chiefly explained by variations in NAR. For long periods and considering the relations among the various traits evidenced by multivariate analysis, the importance of NAR appears less marked, while the morphological traits, namely LAR in determining RGR and LAI for CGR and TGR, assume greater importance.

**Keywords:** potato, biomass allocation, growth analysis, RGR, CGR, TGR, NAR, LAR, LAI, LMR, SLA.

## Introduction

In most herbaceous annuals, field trials have shown that production is determined by the plant's capacity to accumulate dry matter during the vegetative period [1, 2, 3, 4, 5]. Such production depends on leaf area size, on how efficiently the leaf functions, and on the length of the period during which vegetation persists. The assimilates produced by the leaves migrate to accumulation sites, often consisting in harvested plant organs, and thus significantly affect crop yield [6].

In potato, plant development may be divided into periods, controlled genetically and/or by the environment. In accordance with the Canadian Agriculture, Food and Rural Development Department [7], the potato cycle is divided into five growth stages: sprout development (I), plant establishment (II), tuber initiation (III), tuber bulking (IV) and tuber maturation (V). The beginning and

duration of these growth stages depends on environmental factors, such as altitude and temperature, soil, water and nutrient availability, the cultivar and geographical location [8, 9, 10, 11, 12]. Kooman et al. [13] report three phenological stages in the allocation of dry matter accumulating daily. Initially dry matter is partitioned between the leaves and the stem; in the second phase, which starts with the beginning of tuber set, an ever-increasing quantity of dry matter is allocated to the tuber and a decreasing fraction to the leaves and stem; in the third phase all the dry matter produced goes to the tuber. The growth of leaves ceases, and hence photosynthesis, due to leaf senescence. These three phenological phases are affected by climatic factors. The duration of the first phase, including the period between emergence and the beginning of tuber formation, is reduced by short days and by temperatures lower than 20°C. The duration of the



Celestino Ruggiero (Correspondence)



cruggier@unina.it



+39-081-2539124

second phase is also affected by temperature, with an optimum between 16 and 18°C [14] or between 14 and 22°C [15] and by solar radiation [16]. The duration of the senescence phase is reduced by high temperatures, especially above 30°C [17].

Research into potato cultivars is usually limited to analysing differences in tuber yield, yet rarely do such analyses seek to account for the origins of such differences. For an optimal use of natural resources, an explanation for the production differences is important both for physiologists and agronomists [1, 17, 18, 19], in order to obtain useful information for the choice of genotype and the most appropriate agronomic practices to adopt. Indeed, potato cultivars show considerable diversity in terms of growth rates, due to their genetic make-up and their interaction with the environment. Therefore a study of dry matter production and distribution in the various plant organs during development is important to determine a cultivar's growth rate and production. For this purpose, growth analysis has been widely used to study the factors that affect the plant's production and development as the accumulation of photosynthates in time [20].

In field trials, the growth curve of the potato plant normally follows a sigmoidal curve, which does not have a constant pattern, since the growth rate (RGR) varies in relation to field conditions [11, 21, 22, 23]. Moreover, environmental conditions affect the importance of growth components (NAR, LAR, SLA and LMR) in determining the value of RGR [24, 25, 26].

In the literature, there is considerable interest both in defining RGR values for various species and in determining whether differences should be attributed to morphological or physiological factors [1, 17, 27, 28, 29, 30, 31]. The growth of crops, in this case potato, is often considered also in terms of Leaf Area Index (LAI), Crop Growth Rate (CGR) and Tuber Growth Rate (TGR), due to positive correlations between these parameters and tuber production [32, 33]. However, although the above studies are important, research has not generally aimed to shed light on the relations between RGR, CGR, TGR and other parameters, namely LAR, SLA, LMR, NAR and LAI. At the same time, as noted elsewhere [31, 34], RGR as well as CGR and TGR is the result of the interaction of many factors. Indeed, the analysis of only one factor rarely explains the action of each individual factor, since its influence is confused or obscured by others. In such cases, the data need to be examined by means of multivariate analysis techniques.

This research set out to compare, during the different growth phases, the dynamics of dry matter accumulation in nine field-grown potato cultivars, using growth analysis indexes. The main objectives were: (a) to analyse changes over time in RGR, CGR, TGR, NAR, LAR, SLA, LMR and LAI throughout the period from emergence to tuber maturation, and (b) to determine which variables are

most closely associated with variations in RGR, CGR and TGR of the various cultivars.

## Materials and methods

### A. Field trial

Research was conducted during the period February-July 2006 at the Experimental Institute for Tobacco at Scafati (40° 44' 0'' N, 14° 32' 0'' E, 12 m a.s.l.) in the region of Campania (southern Italy). The soil is of a volcanic nature with the following physical and chemical properties: sand 70.2%, silt 18.8%, clay 11%, carbonates 9.4%, organic matter 1.8%, total nitrogen 0.1%, available P<sub>2</sub>O<sub>5</sub> 90 ppm (Olsen method), exchangeable K<sub>2</sub>O 530 ppm (acetate ammonium method), field water capacity 22.9% DW, wilting point 10.9% DW, bulk density 1.38 t m<sup>-3</sup>, electrical conductivity 0.22 m d Sm<sup>-1</sup> and pH of 8.0.

Rainfall during the trial period amounted to 216.4 mm, of which 113.1 mm fell in the first decade of April. The mean minimum ten-day temperature varied from 3.0 to 19.2 °C and the mean maximum from 15.1 to 31 °C. Mean sunlight was 9.3 hours per day, relative humidity varied from 51 to 95%. These data were recorded at the weather station in the same farm where the trial was conducted.

A comparison was made of nine potato cultivars, as reported in table 1, widely grown in the region of Campania. The seed tubers (Ø = 4 cm) obtained from a firm in Scafati were planted on 22 February at a depth of 5-8 cm spaced 25 cm apart on rows 75 cm apart. The plots were distributed according to a randomized block scheme with four replications. The plots, consisting of eight rows 5 m long, were arranged in a continuous line with two rows at the edge. Prior to sowing, the soil was tilled to 40 cm of depth and then harrowed, after applying 50 kg ha<sup>-1</sup> of P<sub>2</sub>O<sub>5</sub>, as perphosphate, and 80 kg ha<sup>-1</sup> of K<sub>2</sub>O as potassium sulphate. Nitrogen was applied after full emergence in the form of ammonium nitrate at the rate of 100 kg ha<sup>-1</sup>. The plots were irrigated regularly to maintain suitable soil moisture levels. All agronomic practices, including insecticide and fungicide treatments, were applied according to practices commonly found in the area.

### B. Data collection

To obtain the primary growth indexes (leaf, stem and tuber dry matter and leaf area), three plants per plot were sampled randomly every week, starting from 18 April, 55 days after planting (DAP), and 20 days after emergence (DAE), roughly at the beginning of tuber set. Emergence was defined when 50% of the plants had visible leaves on the soil surface. The plants were divided into leaves, stem and tubers. Dry matter was determined by oven-drying at 70 °C until a constant weight was reached. Leaf area was measured with an LI-COR-3100 area meter.

### C. Growth parameters

The relative growth rate (RGR), crop growth rate

(CGR), tuber growth rate (TGR), leaf area ratio (LAR), specific leaf area (SLA), leaf area index (LAI) and leaf mass ratio (LMR) for weekly intervals were calculated by using the growth analysis technique [35, 36, 37].

#### D. Statistical analysis

Analysis of variance for all the variables was performed by using SPSS statistics software. The means were compared with Tukey's test at the 5% probability level. The relations among all the indexes considered for all cultivars were analysed through linear correlation, using Statistical for Windows Release 5.1, separately for weekly data, every four and eight weeks. All the data were also analysed using multivariate analysis with the three-stage least squares estimation method [38]. The model adopted set each of the parameters RGR, CGR, TGR, NAR, LAI, LAR, SLA and LMR simultaneously as a variable dependent on all the other parameters, including growth period, and cultivar.

### Results

#### A. Plant dry weight (DW $\text{pt}^{-1}$ )

The increase in total dry matter per plant was curvilinear for the first 30-40 days and then linear until the end of the cycle (Fig. 1a). On average, in the cultivars under observation, from the first to the last sampling (from 55 to 125 DAP) dry matter per plant increased from 3.8 to 194 g. Initially it was connected with the growth of leaf area (LA), which increased until flowering and then progressively decreased (Fig. 1b), together with leaf and stem dry matter (Fig. 1a), with progressive accumulation in the tuber (Fig. 1a). Maximum dry matter per plant at the end of the cycle was observed for "Casanova" and the minimum for cv RZ-90-316 (respectively 205 and 141  $\text{g pt}^{-1}$ ). In general, long-cycle cultivars showed higher leaf area, leaf and stem dry weight from the fifth sampling onwards, up to harvest.

Tuber dry weight followed the trend in plant dry matter (Fig. 1a). On average, in the first five samplings short-cycle cultivars showed higher values than long-cycle; subsequently, long-cycle varieties showed higher tuber growth. However, this does not apply to cultivars RZ-91-450 and RZ-90-318 which showed a lower tuber dry weight per plant than the long-cycle cultivars. The highest tuber dry weight per plant was recorded for the short-cycle cultivar Adora, the lowest for the long-cycle Dali. This parameter was closely correlated with TGR ( $r = 0.98^{**}$ ), less with CGR ( $r = 0.84^{**}$ ), and little with RGR ( $r = 0.13\text{ns}$ ).

#### B. Morphological parameters

##### a. Specific leaf area (SLA), leaf mass ratio (LMR) and leaf area ratio (LAR)

SLA values varied very little both in time and among the cultivars (Fig.2a). The relationship among the values of the nine cultivars was stable over time not

only between two consecutive periods (1 week) but also for two weeks, with values correlated positively and significantly. After 14 days the correlations were still positive, but  $r$  values were non-significant and decreasing in time (data not reported).

LMR values (Fig 2b) were decreasing during the cycle and were on average higher for long-cycle cultivars, especially for Casanova, which recorded the highest values, while the lowest values were observed for RZ-91-450. These differences between the cultivars were very stable in time with a positive correlation and an  $r$  value which was statistically significant throughout the observation period (8 weeks) with a slight exception for the interval 1-5, for which  $r$  was nonetheless fairly high (0.55) (data not reported).

As a consequence of the SLA and LMR values, LAR (Fig 2a) followed the trend of LMR values, decreasing in time and higher for late cultivars. However, in this case the highest values were observed for Dali, the lowest for RZ-90-450. Also for LAR, over time the differences between cvs proved stable, up to a seven-week interval. Only between the first sampling and the others was the correlation weaker, with a stabilisation phase of cultivar traits being observed in the first week (data not reported). The value of LAR appeared more closely linked to that of LMR ( $r = 0.99^{**}$ ), than that of SLA ( $r = 0.21^{**}$ ). However, this was not observed under multivariate analysis (Figs. 4, 5, 6) which in all three cases shows similar coefficients both for LMR and SLA.

##### b. Leaf area index (LAI)

LAI values (Fig. 2b) increased gradually up to the fourth sampling for the early cultivars and up to the sixth for later cultivars, and then gradually diminished in the second part of the cycle. Up to the fourth sampling no considerable differences were observed among the cultivars. However, from the fifth onwards, the late cultivars presented higher LAI values than their early counterparts. The greatest differences were observed between Casanova and RZ-91-450. In time the differences among the cultivars proved stable between two consecutive weeks throughout the period, and up to four weeks, provided that period 4 was not involved, during which the cultivars varied greatly in this parameter. The correlations of LAI values of the different cultivars in the first four periods were negative, reaching a statistically significant value for interval 1-8 (data not reported). This means that the cultivars which had a high LAI in the first four samplings presented low LAI values in the last four. Under multivariate analysis, LAI appeared weakly linked to other factors ( $\text{LAI} = -0.46\text{NAR} + 0.48\text{SLA}$ ,  $R^2 = 0.06$ ), which is why this parameter is considered an exogenous variable.

#### C. Physiological parameters

##### a. Net assimilation rate (NAR)

Albeit with considerable variability from one week to the next, NAR values showed a decreasing trend in time (Fig.3a). The highest values were observed for early cultivars, especially for Safrane, the lowest for late cultivars, with the minimum recorded for Casanova. The relationship between NAR values for the individual varieties in time was shown to be very variable, with no significant correlation between one period and another. Between two successive weeks the correlation was not only very weak, but also negative, which means that the cvs which showed a higher NAR in one week showed a lower NAR the following week (data not reported). In the data set the NAR value was positively and statistically correlated significantly with those of LMR ( $r = 0.35^{**}$ ) and LAR ( $r = 0.38^{**}$ ), and negatively with that of LAI ( $r = 0.34^{**}$ ); with SLA the relation was not significant ( $r = 0.10_{ns}$ ). However, from multivariate analysis of the data (Figs. 4, 5, 6), it emerged that LAR and LAI have a negative effect upon NAR, with a more substantial effect of LAR than LAI. A negative effect was evident, in all three cases, also for sampling, that is, in this case for time.

#### **b. Relative growth rate (RGR)**

Over time also RGR showed a decreasing trend (Fig. 3a), with higher values for long-cycle cultivars and lower for early cultivars, with the exclusion of the first period, during which a higher RGR was found for short-cycle cvs. As with NAR, the relationship between RGR values for the individual varieties in time was very variable, with no significant correlation between one period and the next. Also in this case, between two successive weeks the correlation was not only weak but also negative. This means that the cultivars which showed a higher RGR in one week showed a lower RGR in the following week (data not reported). In the data set, the RGR value was correlated positively and statistically significantly with NAR ( $r = 0.72^{**}$ ) and even more so with LAR ( $r = 0.85^{**}$ ), negatively with LAI ( $r = 0.47^{**}$ ), positively with LMR ( $r = 0.36^{**}$ ), and positively, but not significantly, with SLA ( $r = 0.15_{ns}$ ).

For periods of one week (Tab.2), the correlation between NAR and RGR was positive and highly significant in all the periods considered, while for LAR statistical significance was observed only from the third sampling onward and due to the positive relation between LMR and RGR, while that with SLA appeared almost always negative and never statistically significant, except in the sixth period. For long periods of four weeks, RGR in the first period until flowering did not appear significantly correlated with any of the parameters in question; by contrast, in the second period, between flowering and the end of the cycle, RGR was significantly and positively correlated with all the parameters except SLA. For an interval of eight weeks, the same correlations were observed for the second period, although with NAR the relationship was negative

(Tab. 2).

Moreover, in all the samplings RGR was correlated positively and significantly both with CGR and with TGR (Tabs. 2 and 3). For long periods of four weeks, however, significance was reached only in the interval between flowering and the end of the cycle with TGR, while for the whole interval of eight weeks this occurred only with CGR (Tab. 2). However, for the data set such relations proved weaker, with an  $r$  value of  $0.192^{**}$  for CGR and  $0.197^{**}$  for TGR. Multivariate analysis (Fig. 4) highlights the fact that RGR is dependent both on NAR and on LAR, but with a clear prevalence of LAR, which is even able to negatively affect NAR. As already noted, the latter is also influenced negatively by LAI and by time, with fairly similar coefficients. The figure also shows a direct positive effect of time, albeit not substantial, and that SLA and LMR have no direct influence on RGR, but indirect through LAR and with roughly the same weight.

#### **c. Crop growth rate (CGR)**

As with LAI, CGR values (Fig. 3b) increased until the sixth sampling, fell substantially between the 6th and 7th, and then stayed roughly constant in the last three samplings. On average, higher CGR was observed for the late cultivars, lower for the early cvs except for Adora, which recorded the highest values of CGR. This better CGR performance among the late cultivars was due to the values measured from the fourth sampling onwards, while in the first three it was the short-cycle cultivars which attained higher CGR values. In time, the relationships between the CGR values of each cultivar showed the same pattern as that observed both for NAR and RGR.

Overall, CGR was closely and positively correlated with NAR ( $r = 0.62^{**}$ ) and LAI ( $r = 0.41^{**}$ ), while with LAR the relationship appeared weaker and negative ( $r = 0.24^{**}$ ) due to the negative effect of LMR ( $r = 0.10_{ns}$ ), while the effect of SLA was positive and significant ( $r = 0.15^{**}$ ). In the single periods considered, CGR was always correlated positively and significantly with NAR, while with LAI statistical significance was not reached in the 3rd, 4th and 6th period. With LAR this significance was not reached in the 2nd, 3rd and 4th period, proved negative in the first three periods and then positive. The negativity of this correlation in the early periods was caused by the behaviour of the correlation between CGR and LMR, which at the first sampling was also statistically significant, as it was from the 6th period onwards. By contrast, with SLA the relationship was positive until the 5th period and then negative, but significant only in periods 1 and 6 (Tab.2).

Multivariate data analysis only partly confirms these relationships (Fig. 5), with a positive influence of NAR and negative of LAR. This analysis also shows that CGR is positively conditioned substantially and

directly by LAI and negatively by time, albeit only slightly in the latter case. Also in this case, SLA and LMR have no direct influence on RGR, but indirectly through LAR and with roughly the same weight.

#### **d. Tuber growth rate (TGR)**

The pattern of TGR values (Fig. 3b) shows an increase up to the fifth sampling for short-cycle cultivars and up to the seventh for long-cycle cultivars, and thereafter a reduction for the rest of the cycle.

As with NAR, RGR and CGR, in time the TGR values of the nine cultivars appeared variable with no statistically significant correlation between one period and another. Correlations often proved negative and, as for other parameters, this means that the cultivars which showed a higher TGR in a certain week had a lower TGR in subsequent weeks (data not reported).

Overall, TGR is positively correlated with NAR ( $r = 0.29^{**}$ ), and still further with LAI ( $r = 0.51^{**}$ ), while with LAR the relation appeared negative ( $r = 0.48^{**}$ ) due to the negative relation with LMR ( $r = 0.50^{**}$ ), whereas with SLA the relation proved positive but statistically not significant ( $r = 0.11ns$ ). During the cycle (Tab. 3) the positive relation with NAR always appeared significant, while with LAI it was significant only in periods 1, 2, 6 and 7. The relationship with LAR was negative only in periods 1 and 2 and statistically non-significant only in period 2, in practice due to the behaviour of LMR, which showed a very strong and negative relationship in the first period. The relationship with SLA was almost always positive. Yet it reached the statistical significance threshold only in the first period. For four-week or eight-week periods it is worth noting the non-significance with RGR in the first period until flowering and in the eight weeks overall, that with LAI both in the first part of the cycle and overall, while with NAR the relationship appeared weak in the second part of the cycle, such as to affect the whole period. As with CGR, under multivariate analysis TGR appeared positively dependent on NAR and LAI and negatively on LAR (Fig. 6). In this case, although LAI and NAR have similar coefficients, NAR, in turn, was negatively affected by LAI and by time, and always with the same weight observed for CGR and RGR. LAR acted negatively on NAR always with the same intensity as that observed for RGR and CGR, while on TGR it had a more negative effect than with CGR. The relationships between LAR, SLA and LMR were the same as those observed for RGR and CGR.

#### **Discussion**

As already observed elsewhere in another trial [31], the results of this research highlight the fact that the relationship between the various growth indexes and RGR, CGR and TGR varies both in relation to time,

understood as the interval between measurements, and in relation to the analytical method, that is, whether relations between the parameters are considered on a pairwise basis, independently of other relations, with the simple regression method, or whether they are considered contemporaneously as a whole, with multivariate analysis, with the three-stage least squares method, as in this case. As may be noted from tables 2 and 3, according to the period in question, the relations between the various parameters vary from week to week and also for long periods, whether one considers the first part, second part or the whole cycle.

The data would appear interesting insofar as, while there have been many experiments to identify the parameters that most affect the value of RGR, very few have, to date, also considered parameters like CGR and, for potato, also TGR. These two parameters, in the field of crop science, are most important because they explain the total production of dry matter per area unit, such as CGR, and in the case of potato, whose tubers alone are used, of yield. In this trial we observed that, although RGR is correlated positively both with CGR and TGR, the scale of values of these parameters for the nine cultivars is not the same (Tab. 1), there being cultivars with low RGR yet high TGR and CGR, and vice versa. This is also because the value of RGR during the cycle showed an ever-decreasing trend, while for TGR and CGR this trend appeared to increase until flowering and then decline. During the cycle the parameters in question showed a different behaviour. The physiological parameters (NAR, RGR, CGR, TGR) of the nine cultivars in question proved very variable in time and were never correlated between one period and the other with scale of values between very unstable cultivars, while the morphological parameters (LAR, SLA, LMR and, to a lesser extent, LAI) were found to have scales of values among cultivars which varied slowly during the cycle. This behaviour of the various parameters examined in the field was also observed by Villar et al. [39] on 20 species of *Aegilops* and by Ruggiero et al. [31] on 10 species of legumes and crops. This means that, in the short period of a week, RGR, CGR and TGR are greatly affected by NAR and only slightly affected by morphological parameters. However, for four-week periods and, even more so, eight-week periods, the three indexes, RGR, CGR and TGR, proved positively correlated with morphological traits, especially with LMR, and not with NAR. In this trial, as with another performed with the same method [31], SLA, widely believed to play a major role in defining RGR, does not appear to have played a major role.

There was no great difference in RGR among the cultivars (Tab. 1), with higher RGR values for long-cycle cultivars, which showed these differences chiefly in the central phase of the cycle, whereas at the beginning and end RGR appeared almost the

same. Such differences were subjected to multivariate analysis: they may be attributed both to LAR and NAR, with LAR playing the chief role. The latter is also able to condition NAR (Fig. 4), on which LAI and time have a negative influence. Nevertheless, RGR would not appear to be a very useful parameter to define dry matter production accumulated by the plants at the end of the cycle, which was poorly correlated with this index ( $r = 0.405^*$ ), and even less to determine tuber yield per plant ( $r = 0.247_{ns}$ ). The most explanatory index of total dry matter accumulation was CGR ( $r = 0.99^{**}$ ), somewhat less explanatory TGR ( $r = 0.612^{**}$ ), while total tuber quantity is best explained by TGR ( $r = 0.99^{**}$ ) and least by RGR ( $r = 0.59^{**}$ ).

The cultivars showed higher variability as regards CGR (Tab 1), which increased up to flowering and then decreased. Short-cycle cultivars showed a higher CGR in the first three samplings, while in subsequent samplings it was long-cycle cultivars which showed a higher CGR, with the average value being roughly the same in the two types of cultivar. A similar pattern was observed for LAI. This relationship between CGR and LAI was highlighted by multivariate analysis, the results being shown in figure 5. As may be seen in this figure, LAI plays a key role in determining CGR, both because it acts directly and substantially, and because of its indirect negative effect on NAR. From analysis of the figure it may also be noted that LAR plays an important, albeit negative, role both directly and indirectly through NAR. The negative effects on NAR both of LAI and LAR may be attributed to reciprocal shading of the leaves when leaf area becomes excessive, which means that the crop requires the right sowing density [40, 41], while in crop management it is necessary to control practices that lead both to a deficit and an excess of leaf development. This explains the great interest shown in LAI as regards its interception of light energy and production of plant dry matter [42, 43, 44, 45]. However, both on CGR and on NAR there is the negative effect of time, which may be attributed to an ontogenetic effect, given the reduction in the two parameters as the plant ages.

A similar pattern to CGR was also shown for TGR. By the same token, multivariate analysis of the data (Fig.6) demonstrates the strongly positive influence of LAI on this parameter and the negative influence of LAR, yet without the direct negative effect of time, which nonetheless retains its effect on NAR. In this case, it may be supposed that tuber growth in time does not decline due to ontogenetic factors, but due a reduction in photosynthetic activity resulting from leaf senescence. As regards the direct negative effect of LAR on TGR, we suppose an effect of LMR, which indicates a poor translocation of leaf dry matter to the tuber.

Multivariate analysis (Figs. 4, 5, 6) shows that the equations which define the components of the various factors have a very high correlation

coefficient for all the parameters examined, with the exclusion of NAR which always showed an  $R^2$  of about 0.25. This means that the parameters included in this system (LAR, LAI, SLA, LMR, cultivar and time) explain a limited part of variability of this important physiological parameter, a fundamental component of RGR, CGR and TGR. This had already been noted elsewhere with a similar  $R^2$  to these [31]. However, plant photosynthesis, hence NAR, is known to be greatly affected also by other factors such as radiation, temperature, nutrient availability [45, 46, 47,], water deficit or surplus [47], sowing or transplanting date [48], and leaf integrity. Introduction of mean temperature as a factor of variability did not yield major explanations [32], perhaps also because mean temperature, in these two trials, may be included in the time factor, while other factors remain to be seen. Future research should include these factors in determining growth rates, namely RGR, CGR and TGR.

### Conclusions

This research confirms that the importance of factors determining the growth rates RGR, CGR and TGR varies in relation to the observation period and method of analysis. However, in evaluating CGR and TGR, a decisive role is played by the leaf area index (LAI), a parameter which cannot be included in LAR, which in this case assumes a different role from that played in defining RGR. A particular role is also played by NAR, which in our analysis was poorly defined. A clearer definition of this role is left for future research.

### References

- [1] Van der Zaag, D.E. and Doornbos, J.H. (1987) *Potato Res.*, 30, 551-568.
- [2] Lambers, H. and Poorter, H. (1992) *Adv. Ecol. Res.*, 23, 187-261.
- [3] Lambers, H, Chapin III, F.S., Pons, T.L. (1998) *Plant Physiological Ecology*. Springer, New York, New York, USA.
- [4] Zajac, T., Grzesiak, S., Kuling, B., Poláček, M. 2005. *Acta Physiol. Plant.*, 27, 549-558.
- [5] Tekaling, T. and Hammes, P. S. (2005) *Sci. Hort.*, 105, 13-27.
- [6] Hahn, S.H. (1977) In: Alvin R.T. and Kozłowski T.T., Editors, *Encyclopedia of Tropical Crops*, Academic Press, New York, 237-248.
- [7] Agriculture, Food and Rural Development Department. 2005 Botany of the potato plant. Available on-line at [http://www1.agric.gov.ab.ca/\\$department/deptdocs.nsf/all/pp9547](http://www1.agric.gov.ab.ca/$department/deptdocs.nsf/all/pp9547) Accessed on 17 March 2005.
- [8] Burton, W.G. (1972) In: Rees A.R., Cockshull K.E., Hand D.W. and Hurd G.R. (eds). *The Crop Processes in Controlled Environments*. Academic Press, Inc., London, 217-233.
- [9] Epstein, E. and Grand, W. J., (1973) *Agron. J.*, 65, 400-404.
- [10] Ewing, E.E. (1981) *Am. Potato J.*, 58, 31-49.
- [11] Dawes, D. S., Dwelle, R. B., Kleinkopf, G. E., and Steinhorst (1983) *R. K. Idaho Agric. Exp. Stat. Res.*, pp 717.
- [12] Ezekiel, R. (1990) *Indian J. Plant Physiol.*, 13, 136-140.
- [13] Kooman, P.L., Fahem, M.,P. Tegera, P. and Haverkort A.J. (1996) *Eur. J. of Agron.*, 5, 207-217.
- [14] van Heemst, H.D.J. (1986) *Potato Res.*, 29, 55-66.
- [15] Ingram, K.T; and McCloud, D,E, (1984) *Crop Sci.*, 24, 21-27.

- [16] Demagante, A.L. and Vander Zaag, P. (1988) *Potato Res.*, 31, 73-83.
- [17] Midmore, D.J. (1990) *Potato Res.*, 33, 293-294.
- [18] Çaliskan, M. E., Sarihan, E., Isler, N. and Gunel, E. (1999) Sorrento, Italy, May, 2-7, 371-372.
- [19] Borrego, F., Fernandez, J. M., Lopez, A., Parga V. M., Murillo, M., Carvajal, A. (2000) *Agronomia Mesoamericana*, 11, 145-149.
- [20] Gardner, F.P., Pearce, R.B. and Mitchell, R.L. (1985) In: *Physiology of Crop Plants*. Iowa State Univ. press, USA, 186-208.
- [21] Nečas, J. (1965) *Biologia Plantarum* 7, 180-193.
- [22] Khurana, S.C. and McLaren, J.S. (1982) *Potato Res.*, 25, 329-342.
- [23] Manrique, L.A. (1989) *Am. Potato J.*, 66, 277-291.
- [24] Poorter, H. and Remekes, C. (1990) *Oecologia*, 83, 553-559.
- [25] Atkin, O.K., Botman, B. and Lambers, H. (1996) *Plant Cell Environ.*, 19, 1324-1330.
- [26] Galmés, J., Cifre, J., Medrano, I. and Flexas, J. (2005) *Oecologia* 145, 21-31.
- [27] Garnier, E. and Freijssen, A. (1994) In Roy, J. and E. Garnier (eds.). *A whole plant perspective on carbon-nitrogen interactions*: 267-292. SPB Academic. The Hague.
- [28] Ascione, S., Lombardi, P. and Ruggiero, C. (1996) *Riv. di Agron.*, 30, 594-606.
- [29] Poorter, H. and Van der Werf, A. (1998) H. Lambers, H. Poorter and M. M. I. van Vuren (eds.) *Backhuys Publishers, Leiden*, 309-336.
- [30] Poorter, H., Garnier, E. (1999) In *Handbook of Functional Plant Ecology* Eds. F. Pugnaire and F. Valladares, 82-120. Marcel Dekker Inc., New York.
- [31] Ruggiero C., Ascione S., Punzo A. and Vitale C. (2012) *J. of Crop Sci.*, 3, 57-63.
- [32] Gordon, R., Brown, D.M., and Dixon, M.A. (1997) *Potato research*, 40, 251-256.
- [33] Boyd, N.S., Gordon, R. and Martin, R.C. (2002) *Potato Research*, 45, 117-129.
- [34] Kruger, E.L. and Volin, J.C. (2006) *Funct Plant Biol*, 33, 421-429.
- [35] Radford, P.J. (1967) *Crop Sci.* 7, 171-175.
- [36] Evans, G.C (1972) *The quantitative analysis of plant growth*. University of California Press, Berkeley.
- [37] Hunt, R. (1982) *Basic Growth Analysis*. Unwin Hyman Ltd, London, pp 112.
- [38] Wooldridge, J.M. (2002) *Econometric Analysis of Cross Section and Panel Data*. Cambridge, MA, MIT Press.
- [39] Villar, R, Marañón, T, Quero, J. L., Panadero, P., Arenas, F. and Lambers, H. (2005) *Plant and Soil* 272, 11-27.
- [40] Sarkar, R.K. and Pal, P.K. (2005) *Ind. J. Agric.Sci.*, 75, 143-146.
- [41] Hussain, I., Ayyz, K.M. and Khan, H. (2010) *Sarhad J. Agric.* 26, 169-176.
- [42] Burton, W.G. (1981) *Am. Potato J.*, 58, 3-14.
- [43] Niczyporowicz, A.A. (1984) *Acta Physiol.Plant.*, 6, 105-126.
- [44] Dehdashti, S.M. and Riahinia, S. (2008) *J of Biol. Sci.*, 8, 908-913.
- [45] Sarkar, R.K., Pal, P.K. (2005) *Ind. J. of Agri. Sci.*, 75, 143-146.
- [46] Saleem, M., Maqsood, M., Javaid, A., Hassan, M.U. and Khaliq, T. (2010) *Pak. J. Bot.*, 42, 3659-3669.
- [47] Haruna, J.M. (2011) *J. of An. & Plant Sci.*, 21, 653-659.
- [48] Baloch, M.S., Awan, I.U. Assan, G. (2006) *J. Zhejiang Univ Sci. B*, 7, 572-579.

### Figure captions

Figure 1. Average trend of dry matter in the plant, leaves, stem and tubers (a) and leaf area (b) in the various periods. Vertical bars represent standard deviations.

Figure 2. Average trend of LAR, SLA (a), LMR and LAI (b) in the various periods. Vertical bars represent standard deviations.

Figure 3. Average trend of RGR, NAR (a), CGR and TGR in the various periods. Vertical bars represent standard deviations.

Figure 4. Cause-effect relationships among growth variables for RGR, data for the whole period. The numbers are the parameter coefficients of the equations tested by the three-stage least squares estimation method; analysis carried out with data values normalized on the average of the single parameter. The constants of the equations and adjusted  $R^2$  are, respectively, -0.57 and 0.91 for RGR, 0 and 0.68 for SLA, 0 and 0.99 for LMR, 0 and 0.99 for LAR, and +0.81 and 0.25 for NAR.

Figure 5. Cause-effect relationships among growth variables for CGR, data for the whole period. The numbers are the parameter coefficients of the equations tested by the three-stage least squares estimation method; analysis carried out with data values normalized on the average of the single parameter. The constants of the equations and adjusted  $R^2$  are, respectively, +0.30 and 0.83 for CGR, 0 and 0.66 for SLA, 0 and 0.99 for LMR, 0 and 0.99 for LAR, +0.81 and 0.25 for NAR.

Figure 6. Cause-effect relationships among growth variables for TGR, data for the whole period. The numbers are the parameter coefficients of the equations tested by the three-stage least squares estimation method; analysis carried out with data values normalized on the average of the single parameter. The constants of the equations and adjusted  $R^2$  are, respectively, 0 and 0.71 for TGR, 0 and 0.66 for SLA, 0 and 0.99 for LMR, 0 and 0.99 for LAR, +0.79 and 0.25 for NAR.

### Table legends

**Table 1.** RGR, CGR, TGR mean values of the growth parameters for all cultivars and for the total growth period. Values with different letters are statistically significant at the 5% level.

**Table 2.** Pearson correlation coefficients between RGR and CGR and their growth components in each of the growth periods of 56, 28 and 7 days. Values in bold are significant at the 5% level.

**Table 3.** Pearson correlation coefficients between TGR and its growth components in each of the growth periods of 56, 28 and 7 days. Values in bold are significant at the 5% level.

**Table 1.** RGR, CGR, TGR mean values of the growth parameters for all cultivars and for the total growth period. Values with different letters are statistically significant at the 5% level.

Cultivar	Initial M g pt <sup>-1</sup>	RGR mg g <sup>-1</sup> d <sup>-1</sup>	CGR g m <sup>2</sup> d <sup>-1</sup>	TGR g m <sup>2</sup> d <sup>-1</sup>	SLA cm <sup>2</sup> g <sup>-1</sup>	LMR g g <sup>-1</sup>	LAR cm <sup>2</sup> g <sup>-1</sup>	LAI	NAR g m <sup>2</sup> d <sup>-1</sup>
Adora	6.49a	61.29	17.82a	17.01a	211.79ab	0.26c	57.09bc	1.94abc	0.96ab
Carrera	3.89b	68.23	15.88ab	14.60ab	199.31b	0.27c	54.56c	1.50c	1.10a
Casanova	2.80b	61.30	15.37ab	12.15bc	203.90ab	0.35a	70.82a	2.57a	0.69b
Red-Star	2.97b	58.98	14.46b	12.35c	204.46b	0.28ab	58.10abc	1.89abc	0.84b
Dalì	3.32b	59.56	14.20b	11.47bc	190.47ab	0.32bc	63.25bc	1.93bc	0.77ab
Rz 90-316	3.65b	64.96	13.06b	12.17bc	199.05b	0.28bc	54.98c	1.51c	0.96ab
Rz 91-450	3.92b	64.42	13.09b	12.44bc	228.38a	0.25c	57.72bc	1.41c	0.98ab
Safrane	4.57ab	63.99	15.19ab	14.27abc	228.70a	0.26c	60.91abc	1.46c	1.11a
Victoria	2.61b	62.62	15.38ab	12.51bc	200.61b	0.33ab	65.93ab	2.19ab	0.79b
		n.s.							

**Table 2.** Pearson correlation coefficients between RGR and CGR and their growth components in each of the growth periods of 56, 28 and 7 days. Values in bold are significant at the 5% level.

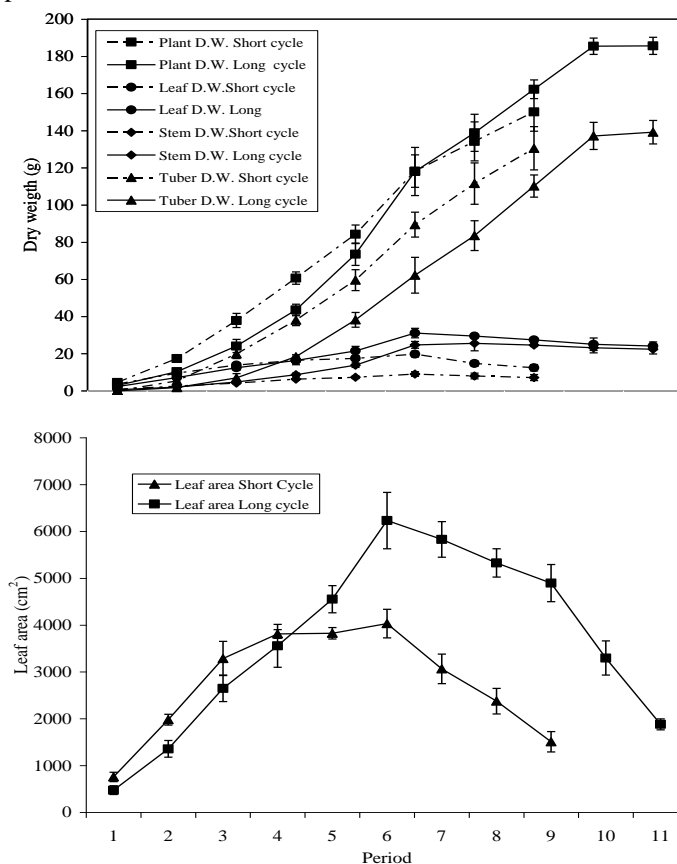
Growth period	Components										
	RGR LAR	RGR LMR	RGR SLA	RGR LAI	RGR NAR	CGR LAR	CGR LMR	CGR SLA	CGR LAI	CGR NAR	CGR RGR
1→8	<b>0.63</b>	<b>0.66</b>	0.08	<b>0.67</b>	<b>-0.67</b>	<b>0.45</b>	<b>0.45</b>	0.13	<b>0.65</b>	<b>-0.37</b>	<b>0.45</b>
1→4	0.03	0.10	-0.23	0.14	0.08	<b>-0.50</b>	<b>-0.51</b>	0.14	<b>0.46</b>	<b>0.54</b>	0.16
5→8	<b>0.52</b>	<b>0.53</b>	-0.16	<b>0.42</b>	<b>0.41</b>	<b>0.58</b>	<b>0.58</b>	0.19	<b>0.63</b>	0.29	<b>0.89</b>
1	-0.31	<b>-0.44</b>	0.15	0.26	<b>0.91</b>	<b>-0.37</b>	<b>-0.67</b>	<b>0.38</b>	<b>0.79</b>	<b>0.77</b>	<b>0.74</b>
2	0.16	0.19	-0.15	0.05	<b>0.89</b>	-0.28	-0.31	0.19	<b>0.70</b>	<b>0.75</b>	<b>0.67</b>
3	<b>0.34</b>	<b>0.35</b>	-0.13	-0.21	<b>0.88</b>	-0.10	-0.14	0.19	0.27	<b>0.85</b>	<b>0.75</b>
4	<b>0.38</b>	<b>0.33</b>	-0.02	-0.07	<b>0.90</b>	0.16	0.12	0.05	0.17	<b>0.88</b>	<b>0.88</b>
5	<b>0.50</b>	<b>0.44</b>	0.08	<b>0.33</b>	<b>0.82</b>	<b>0.40</b>	0.31	0.05	<b>0.44</b>	<b>0.81</b>	<b>0.94</b>
6	<b>0.34</b>	<b>0.42</b>	<b>-0.38</b>	0.20	<b>0.79</b>	<b>0.33</b>	<b>0.42</b>	<b>-0.40</b>	0.31	<b>0.76</b>	<b>0.94</b>
7	<b>0.45</b>	<b>0.47</b>	-0.12	<b>0.44</b>	<b>0.67</b>	<b>0.46</b>	<b>0.49</b>	-0.17	<b>0.52</b>	<b>0.60</b>	<b>0.98</b>
8	<b>0.36</b>	<b>0.33</b>	0.01	0.24	<b>0.74</b>	<b>0.40</b>	<b>0.38</b>	-0.01	<b>0.33</b>	<b>0.71</b>	<b>0.99</b>



**Table 3.** Pearson correlation coefficients between TGR and its growth components in each of the growth periods of 56, 28 and 7 days. Values in bold are significant at the 5% level.

Growth period	Components						
	TGR RGR	TGR CGR	TGR LAR,	TGR LMR	TGR SLA	TGR LAI	TGR NAR
1→8	0.20	<b>0.60</b>	0.31	<b>0.38</b>	0.04	0.16	0.31
1→4	0.07	<b>0.83</b>	<b>-0.82</b>	<b>-0.84</b>	0.20	0.01	<b>0.79</b>
5→8	<b>0.93</b>	<b>0.80</b>	<b>0.58</b>	<b>0.57</b>	0.11	<b>0.46</b>	0.26
1	<b>0.47</b>	<b>0.79</b>	<b>-0.58</b>	<b>-0.94</b>	<b>0.47</b>	<b>0.57</b>	<b>0.67</b>
2	<b>0.78</b>	<b>0.82</b>	-0.02	-0.03	0.07	<b>0.42</b>	<b>0.75</b>
3	<b>0.89</b>	<b>0.58</b>	<b>0.49</b>	<b>0.53</b>	-0.25	-0.22	<b>-0.70</b>
4	<b>0.94</b>	<b>0.88</b>	<b>0.35</b>	<b>0.33</b>	-0.07	0.01	<b>0.83</b>
5	<b>0.92</b>	<b>0.83</b>	<b>0.40</b>	0.31	0.19	0.18	<b>0.78</b>
6	<b>0.68</b>	<b>0.71</b>	<b>0.43</b>	<b>0.48</b>	0.27	<b>0.39</b>	<b>0.45</b>
7	<b>0.81</b>	<b>0.88</b>	<b>0.64</b>	<b>0.61</b>	0.06	<b>0.64</b>	<b>0.34</b>
8	<b>0.92</b>	<b>0.91</b>	<b>0.36</b>	<b>0.35</b>	0.01	0.26	<b>0.65</b>

Figure 1. Average trend of dry matter in the plant, leaves, stem and tubers (a) and leaf area (b) in the various periods. Vertical bars represent standard deviations.



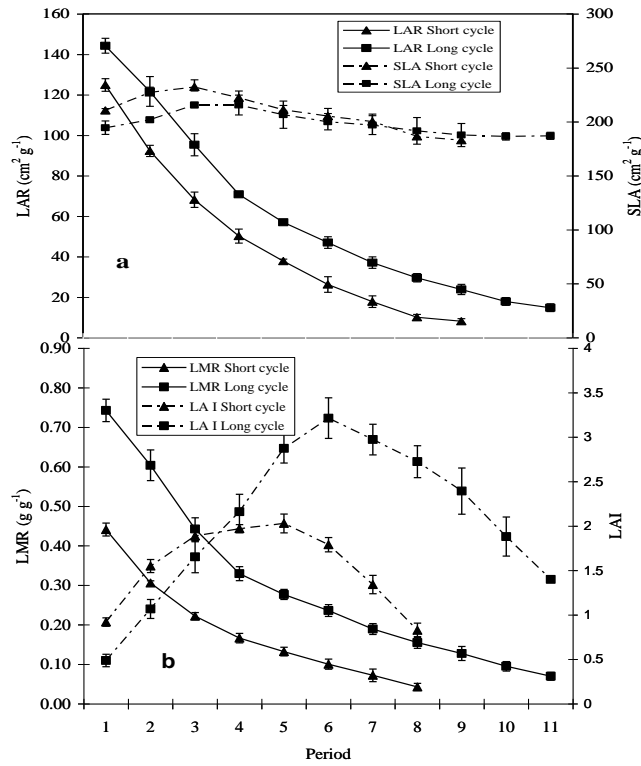


Figure 2. Average trend of LAR, SLA (a), LMR and LAI (b) in the various periods. Vertical bars represent standard deviations.

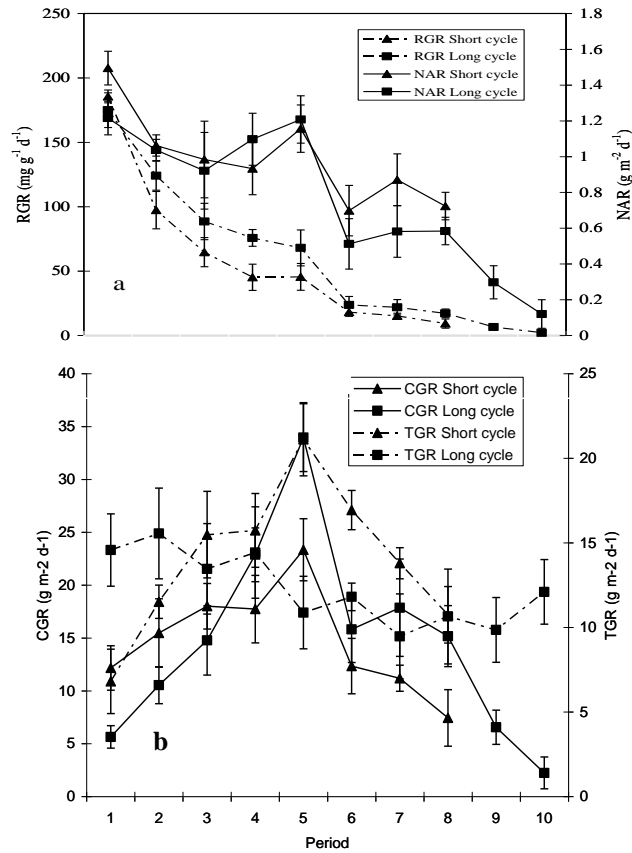


Figure 3. Average trend of RGR, NAR (a), CGR and TGR in the various periods. Vertical bars represent standard deviations.

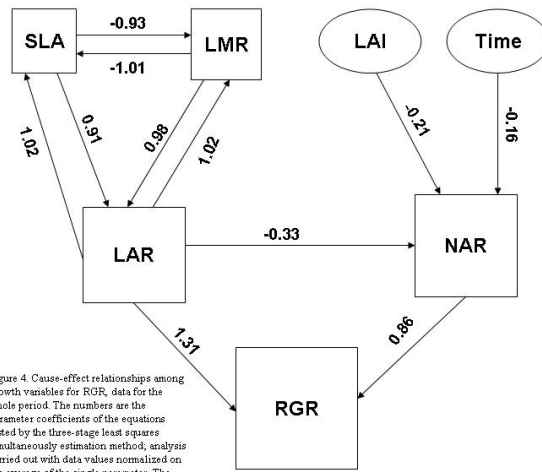


Figure 4. Cause-effect relationships among growth variables for RGR, data for the whole period. The numbers are the parameter coefficients of the equations tested by the three-stage least squares simultaneously estimation method, analysis carried out with data values normalized on the average of the single parameter. The constants of the equations and adjusted R2 are, respectively: -0.57 and 0.91 for RGR, 0 and 0.62 for SLA, 0 and 0.99 for LMR, 0 and 0.99 for LAR, +0.81 and 0.25 for NAR.

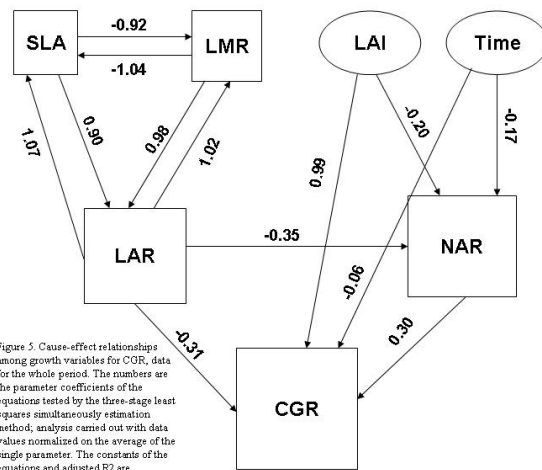


Figure 5. Cause-effect relationships among growth variables for CGR, data for the whole period. The numbers are the parameter coefficients of the equations tested by the three-stage least squares simultaneously estimation method, analysis carried out with data values normalized on the average of the single parameter. The constants of the equations and adjusted R2 are, respectively: +0.30 and 0.83 for CGR, 0 and 0.66 for SLA, 0 and 0.99 for LMR, 0 and 0.99 for LAR, +0.81 and 0.25 for NAR.

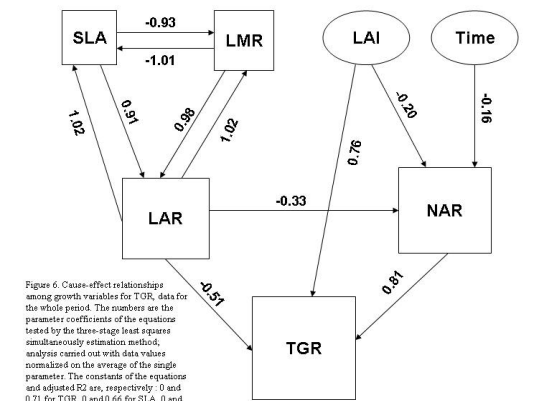


Figure 6. Cause-effect relationships among growth variables for TGR, data for the whole period. The numbers are the parameter coefficients of the equations tested by the three-stage least squares simultaneously estimation method, analysis carried out with data values normalized on the average of the single parameter. The constants of the equations and adjusted R2 are, respectively: 0 and 0.71 for TGR, 0 and 0.66 for SLA, 0 and 0.99 for LMR, 0 and 0.99 for LAR, +0.79 and 0.25 for NAR.