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How Photoperiod Affects Growth Rate and Biomass Allocation Pattern: a Comparative Study on Three Genotypes of *Arabidopsis thaliana*

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Abstract: This study examines the rate of change in dry weight and the way in which the change is distributed between various parts of the plants in response to photoperiod. Classical growth analysis was used to study how relative growth rate, net assimilation rate, leaf area ratio, specific leaf area and biomass allocation to leaves, stems, petioles and roots respond to day length. Significant effect of day length was found on almost all the growth parameters except the biomass allocation to roots. The plants grown under 16 hours show higher growth rate (RGR) than those in 8 hours photoperiod. This high RGR is achieved by high net assimilation rate (NAR) and low specific leaf area: a component of leaf area ratio. Low specific leaf area and high NAR reflect the anatomical modifications of leaf in response to day length, which increase the physiological activities per unit leaf area. Plants grown under long day condition invest more biomass to the stems, little to the leaves and show no clear tendency for roots.

Key words: Photoperiod, growth rate, biomass allocation, *Arabidopsis*

Introduction

Plants can respond dramatically to small scales temporal and spatial variation in habitat quality. Pulses of light can trigger physiological and morphological responses that enable the plants to adjust effectively to temporal changes in their environment. Plants are assumed to respond by altering growth and /or adjusting biomass partitioning to various organs (Moony and Winner, 1991; Dale and Causton, 1992; Meekins *et al*., 2000). Low light availability for instance, leads to reductions in biomass allocation to root (RWR), relative growth rate (RGR) (Dale and Causton, 1992; Robinson and McCarthy, 1999) and increase in leaf weight ratio (LWR) (Abrahamson and Gadgil, 1973; Givnish, 1982; Stutzel *et al*., 1988; Anten and Hirose, 1999). In addition, leaf area per unit leaf mass (specific leaf area, SLA) is generally found to decrease with increasing light availability (Bjorkman, 1981; Dijkstra, 1989; Anten and Werger, 1996). Thus, leaf area per unit of plant dry weight (leaf area ratio, LAR), which is the product of LWR and SLA, can be expected to decrease as light availability increase (Causton and Venus, 1981).

Virtually every aspect of plant growth and development is influenced by light availability. Numerous publications have reported leaf expansion, increased leaf succulence, stem elongation and alteration in root to shoot ratio (Salisbury and Ross, 1986; Wilson, 1988; Meekins *et al*., 2000). Many studies have investigated effects of photoperiod on organic acids, chlorophyll content, flower induction, seed development and seed filling, and thus yield of agricultural plants. Here, we focus on the rate of change in dry weight and the way in which the change is distributed between various parts of the plant in response to photoperiod. The present investigation will provide more insight into the causation of genotypic differences in growth rate. In particular, we wanted to (I) see how photoperiod affect growth rate and biomass patterns and (ii) to what extent the plants optimize their performance for maximizing NAR under contrasting photoperiods.

Materials and Methods

The experiment was conducted at the University of Wales, Aberystwyth, UK. The seeds used were the mutants obtained from the wild type population of *Arabidopsis thaliana* (L.) by chemical mutagenesis using ethyl-methane-sulphonate (Harpham *et al*., 1991). Seeds of three genotypes: Wild type, eti 5, eti 10, were raised under uniform conditions. Initially, five seed genotype^{-1} were placed on the surface of damp Levington`s Seed Compost No.1 in 1 dm^3 plastic pots on March 1994. There were five replicate pots per genotype per treatment and harvest. After one week when the cotyledons spread apart and the first leaf was just visible, extra seedlings were removed carefully leaving behind one plant per pot. The plants were then shifted to controlled-environment Saxcil growth chambers. Illumination to the growing plants in these chambers was provided by 80 Watt warm white and 60 watt incandescent bulbs (Philips) that provided photosynthetically active radiation (PAR) of 89 μmol m^{-2} s^{-1}. Growth chambers were adjusted to provide temperature of 20°C during the day and 15 °C at night. Two weeks after sowing, a short day-length, (8 hour) was given to one group of plants and was designated as short-day treatment. For the second group of plants, a long day-length (16 hours) was chosen for the long day treatment. The arrangement was made to ensure that each plant received similar experimental level of radiation with minimal shading by plants in adjacent pots. The plants were watered regularly to keep the compost slightly moist. The duration of the experiment was fixed at four weeks, keeping in mind that pot-bound plants did not suffer an obvious check on growth and to ensure that some genotypes growing in long day condition were still near their exponential phase of growth at the end of the growth measurements. The experiment consisted of two light treatments, five weekly harvests, three genotypes and five replicates (in randomized block). Growth parameters were determined by harvesting five plants of each genotype, one from each block on 7, 14, 21 and 28 days after transferring into the growth chamber. At each harvest, plants were separated into roots, leaves and stem, including leaf petioles because they were too small to be distinguished from the stem especially in the first harvest and were estimated with the stem in all the subsequent harvests. Leaf areas were measured with photoelectric area meter (*Delta-T*, MK2 model). All plant parts were then oven-dried at 80 °C and their dry weight measured after 48 hours.

Relative growth rates (RGR: day^{-1}), net assimilation rate (NAR: g cm^{-2} day^{-1}) and partitioning of biomass between different organs in terms of weight ratios were calculated according to the Classical Growth Analysis (Causton and Venus, 1981). Briefly, RGR was calculated by dividing the difference in log-transformed plant dry weight between the two harvests by the time difference between those harvests. This forms the basis for calculation of the net assimilation rate (RGR = NAR x LAR). The portioning of biomass between different organs was determined by expressing the dry weight attributable to particular organ as a quotient of total plant dry weight, and this is termed 'weight ratio' for that organ. Species, treatments and harvests for all ratios and rates were compared by analysis of variance by using purpose written soft ware. Interaction between treatments and plant age (harvests) are presented as graphs with significant differences indicated by bars of least significant difference (LSD), derived from Duncan's (1955) Tables. The relationship between genotypes and photoperiodic treatments was investigated in two-way tables also utilizing Duncan's Multiple Range tests. Explanation of the growth, biomass allocation and leaf parameters included in this study.

RGR is an increase in dry weight per plant dry weight, NAR is the net gain in dry weight per unit of the leaf area, LAR is the relative amount of biomass, a plant invest in leaf area, SLA is the quotient of total leaf area to total leaf dry weight, LWR is the weight of the leaf as proportion of whole plant, SWR is the weight of the stem as a proportion of whole plant, RWR is the weight of the root as a proportion of whole plant.

Results

Relative growth rate and its components (NAR and LAR) The results (Table 1) revealed that day length and harvest (Plant age) were the source of most variability in RGR ($P < 0.001$). When the time course graphs were drawn for each mutant the pattern observed was unclear and complex. To simplify the

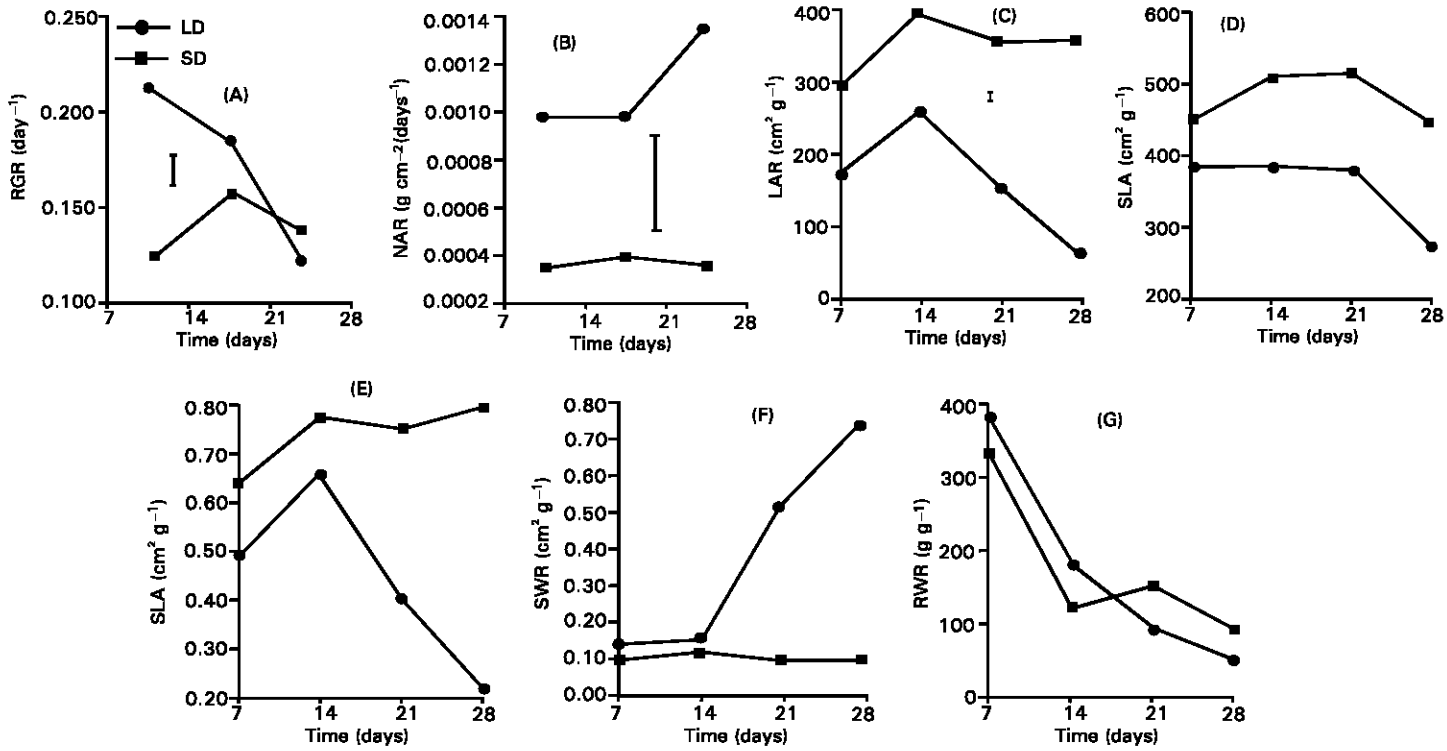

Fig. 1: Effect of day length on (A) relative growth rate (RGR), (B) net assimilation rate (NAR), C) leaf area ratio (LAR), (D) specific leaf area (SLA), (E) Leaf weight ratio (LWR) (F) stem weight ratio (SWR) and (G) root weight (RWR) of *Arabidopsist thaliana* genotypes

comparison of the responses of RGR to photoperiod, graphs were drawn of the mean genotype values for each of the light periods (Fig.1a and Table 2). These results clearly demonstrate that a reduction in light period led to a significant ($P < 0.05$) fall in the RGR of all the genotypes. The highest RGR was found in the long day grown plants (LD) at the beginning of the experiment but did not persist in successive harvests (ontogenetic drift). Consequently, at the end of experiment no significant difference in RGR was found between the two light treatments. The genotypes differed significantly ($P < 0.05$) in mean RGR. *eti* 5 had a significantly lower RGR than either *eti* 10 and Wild type which did not differ significantly from each other.

Physiological activity per unit leaf area (NAR) was significantly (Table 1) influenced by photoperiod. NAR in all the three genotypes was significantly lower under short day conditions (SD). Although the NAR of genotype grown in long day condition (LD) showed a slight increase in the later part of the experiment (Fig. 1b), these changes in NAR with time were not significant (Table 1). Unlike RGR, no genotype differences were found for this growth parameter.

Contrary to NAR, genotypes differed significantly ($P < 0.001$) in mean LAR, Wild type having the highest value (279.65 cm^2g^{-1}), *eti* 10 being intermediate (258.38 cm^2g^{-1}), and lowest in *eti* 5 (225.74 cm g^{2-}).[1] In contrast to the previous two parameters, a reduction in photoperiod caused a significant increase in LAR of all the genotypes. Fig.1c indicates that during the first three weeks of the experiment, LAR showed a significant rise followed by a significant decline in both the treatments, but the magnitude of decline was greater in plants grown under LD than SD. By the end of the experiment, the LAR in SD plants remained consistent while that of LD grown plants continued the steady decline. These time- associated changes in LAR were responsible for the occurrence of a significant photoperiod x genotype interaction (Table 1).

Specific leaf area (SLA) was significantly higher in SD than LD in all the genotypes (Table 2). Although all the genotypes reacted similarly in the response of SLA to photoperiod, the mean SLA was higher in *wild type* (538.22 cm^2g^{-1})than eti 5 (407.31 cm^2g^{-1}) and eti l10 (413.15 cm^2g^{-1}) which did not differ significantly between each other (Table 2). The ontogenetic trends of plants were sufficiently influenced by the day length as indicated by existence of significant interaction between photoperiod and plant age (Table 1). SLA was consistently higher in SD than LD during the experiment. Under SD the SLA showed an initial significant increase and then a week of stability before the final drop at the end of the experiment. On the other hand under LD, the SLA remained stable in the first two weeks and underwent a significant drop only during the last week of the experiment (Fig.1d).

Ratios of biomass allocation to leaf, stem and root: The LWR showed a significant response to day length (Table 1) but all the genotype reacted similarly. An eight hours photoperiod promoted the LWR significantly in all the genotypes. *eti* 5 had significantly lower LWR than the other two genotypes which did not differ between themselves (Table 2). Fig. 1e shows that the ontogenetic changes in LWR mirrored the changes found in LAR. In SD, there was a significant increase in LWR during the first two weeks of the experiment and remained insensitive to ontogenetic changes during the rest of the experimental period. LD plants showed an initial rise but contrary to the SD treatment, the LWR in LD showed a steady decline in the later part of the experiment. These inter-harvest differences in response of LWR to photoperiod were responsible for the presence of day length x harvest significant interaction (Table 1). The genotypes respond differently to photoperiod in terms of biomass allocation to stem. For SWR, the wild type decreased by 68%, *eti* 10 by 74% and *eti* 5 by 80% when plants were grown in SD as compared to LD. Therefore the mean values of SWR did not differ between the genotypes. Contrary to all the above parameters of growth and biomass allocation, the main effect of photoperiod was not significant for RWR (Table 1). Genotypic differences in RWR were observed in response to photoperiod. Contrary to other genotypes, RWR increased in *eti* 5, grown under SD and is responsible for the significant interaction between genotype and photoperiod in the overall analysis (Table 1). During the course of plant development, the differences in RWR between LD and SD appeared at one time (harvest) and disappeared at the other (Fig. 1g), causing an interaction between harvest and photoperiod significant in the overall analysis.

Table 1: F- values of relative growth rate (RGR), net assimilation rate (NAR), leaf area ratio (LAR), specific leaf area (SLA), leaf weight ratio (LWR), stem weight ratio (SWR) and root weight ratio (RWR) of four genotypes of *A. thaliana* (G) grown at two different day lengths (D). The results are analyzed from the data obtained from five weakly harvests (H) and five replicates.

	RGR	NAR	LAR	SLA	LWR	SWR	RWR
D	29.65***	43.43***	1451.25***	380.74***	895.74***	1483.42***	1.40
G	4.79*	<1	21.37***	13.39**	6.89**	<1	6.41**
D x G	<1	<1	1.12	<1	<1	10.65***	11.78***
H	19.08***	1.19	102.46***	37.46***	88.34	376.19***	160.54***
D x H	23.66***	1.33	66.98***	5.19**	120.28	403.84***	26.86***
G x H	6.58***	<1	7.60***	5.57***	3.72	3.96**	4.44***
H x D x G	1.84	<1	1.34	2.53*	2.19	3.48**	9.48***

* P <0.05, ** P< 0.01, *** P < 0.001

Table 2: Mean values of growth parameters for four genotypes of *A. thaliana* grown under two different photoperiods (long day & short day), averaged across five harvests and five blocks. Values that are not significantly different at P< 0.05 have the same superscript letters.

Growth parameters	Photoperiod		
	Long day	Short day	Mean
RGR (day^{-1})			
wild type	0.1769c	0.1467ab	0.1618
eti 5	0.1617bc	0.1217a	0.1417
eti 10	0.1778c	0.1467ab	0.1592
Mean	0.1720	0.1383	
NAR ($g\ cm^{-2}\ day^{-1}$			
Wild type	0.001036c	0.000375a	0.000705
eti 5	0.001155c	0.000343a	0.000749
eti 10	0.000819bc	0.000406ab	0.000613
Mean	0.000911	0.000374	
LAR ($cm^{-2}\ g^{-1}$)			
Wild type	175.83b	383.47e	279.65
eti 5	143.50a	307.98c	225.74
eti 10	161.45ab	355.30d	258.38
Mean	160.26	348.92	
SLA ($cm^{-2}\ g^{-1}$)			
Wild type	371.85a	504.58c	538.22
eti 5	348.03a	466.58b	407.31
eti 10	350.15a	476.15b	413.15
Mean	356.68	482.44	
LWR			
Wild type	0.4637a	0.7603b	0.6119
eti 5	0.4273a	0.7079b	0.5676
eti 10	0.4426a	0.7660b	0.5943
Mean	0.4445	0.7380	
SWR			
Wild type	0.3593b	0.1153a	0.2373
eti 5	0.4074c	0.0805a	0.2439
eti 10	0.3748b	0.0958a	0.2353
Mean	0.3804	0.0972	
RWR			
Wild type	0.1770c	0.1250ab	0.1510
eti 5	0.1651c	0.2115a	0.1883
eti 10	0.1826c	0.1581bc	0.1703
Mean	0.1749	0.1698	

Discussion

Effect of photoperiod on RGR: Relative growth rate is regulated by two primary factors: the efficiency of the leaves (NAR) and the ratio of leaf biomass to whole plant biomass (LAR) (Causton and Venus, 1981). We observed that mutants of *Arabidopsis* grown under 8 hours photoperiod exhibited a low RGR. The low RGR of eti mutants grown under SD condition is due to low NAR and high LAR. This opposite trend of the two components of RGR is not surprising, but could imply that both the factors regulate growth interdependently. Such a dependency could indicate a functional balance between plant leafiness and the assimilation efficiency of the leaves. A possible explanation for the inverse relationship between NAR and LAR could be the amount of compounds involved in photosynthesis. A high NAR can be achieved by high rate of photosynthesis. This requires a large amount of enzymes and light harvesting complexes per unit leaf area and possibly an extra layer of photosynthetic tissue, all of which decrease SLA and thus LAR (Poorter, 1989; Koning, 1989). The low NAR under short-day conditions might be the result of high SLA. High SLA (thinner lamina or lower tissue density or both) reflects a faster potential rate of return on investment in leaves and low rate of photosynthesis per unit leaf area (Bunce, 1986).

SLA decreased with increasing photoperiod. This result agrees with findings of Dijkstra, 1989; Anten and Werger (1996) which suggest light availability to be the major factor in determining the SLA. Low SLA and high NAR in LD plants might result from greater number of mesophyll cells per unit leaf area (Koning, 1989). Thus the assumption that can be put forward from this study is that photoperiod influences the RGR through the anatomical modifications that increase the physiological activity per unit leaf area. The causes of this relationship remain to be fully established, but it is of importance that an increase in mesophyll tissue can decrease SLA and thus LAR (Koning, 1989).

Plants grown under long day conditions allocated biomass more to the stem (SWR) while the SD plants invested more to the leaves (LWR) and no significant differences between LD and SD was found for RWR. This pattern of biomass allocation reflects a trade-off between growth of stem and allocation of mass to leaves. This result is consistent with various other studies (McMahon, 1973; Givnish, 1982; Menges, 1987; Stutzel *et al.*, 1988; Anten and Hirose, 1999). A rapid increase in SWR in the later part of experiment may be associated with the switch to reproductive development. During reproductive phase, rosette plants often invest more in stem elongation rather than foliar structure (Causton and Venus, 1981). Considering the pattern of biomass allocation to roots, it may be concluded that for roots the environmental stimuli are predominantly soil temperature and moisture rather than photoperiod (Head, 1973). On the whole, the results (Tables 1 and 2) confirm that *Arabidopsis thaliana* is a long-day plant (Salisbury and Ross, 1986) and small genetic changes made in the present investigation are unable to modify the sensitivity of its genotypes to day length.

Variations in RGR between the genotypes: Apart from the effect of photoperiod on RGR, significant differences between the genotypes are found. Genotypic variation in RGR is largely linked with LAR. The genotypes with high RGR (wild type) also have high LAR (Table 2). As RGR is a product of NAR and LAR, no significant difference between the genotypes for the former parameter is found. Therefore, genotypic differences in RGR may be totally attributed to variation in LAR. The importance of LAR in determining the intra-specific differences in RGR found in this study, confirm the results obtained by Roetman and Sterk (1986) in *Taraxacum* and in two inbred lines of *Plantago major* by Dijkstra and Lambers (1986). Having shown that LAR is important in explaining differences in the mean RGR between the genotypes, a further analysis of this factor is imperative. The results (Table 2) show that genotypes of *Arabidopsis* differ both in the allocation of biomass in the leaves (LWR), and in the amount of leaf area constructed per unit leaf weight (SLA). The allocation of dry matter to LWR and SLA is systematically higher in mutants with higher LAR. The higher LAR values and thus the RGR are attributed by both higher SLA and LWR (components of LAR). The genotypic differences for both the parameters can be ascribed either to morphological factors (thickness of the leaves, veins structure, supporting tissues) or to the chemical composition of leaf (Dijkstra, 1989).

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