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PATTERN OF DEFOLIATION AND ITS EFFECT ON PLANT PERFORMANCE AND BIOMASS PARTITIONING IN *ABELMOSCUS ESCULENTUS*

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Abstract: Three experiments were performed to examine the effect of defoliation on plant performance and biomass partitioning among different plant modules. Different patterns of tissue removal were used to simulate natural herbivore damage in *Abelmoscus esculentus* (L.). Plants were subjected to removal of tissues from either a single leaf or throughout the plant. The effect of defoliation on plant performance and biomass allocation was quantified by using Classical Growth Analysis Technique. Both levels of defoliation and patterns of tissue removal effect growth performance of *Abelmoscus esculentus*. Temporal compensatory changes in relative growth rate were mediated by similar changes in net assimilation rate (NAR). The ontogenetic changes in leaf area ratio (LAR) to defoliation were largely determined by changes in specific leaf area (SLA) rather than leaf weight ratio (LWR) during the experimental period. All defoliation treatments show initial shifts of biomass from leaves to stems and roots but eventually reached to the level of control (un-defoliated) plants with the passage of time i.e. they show compensatory changes.

Keywords: *Abelmoscus esculentus*, biomass partitioning, defoliation patterns, leaf attributes, net assimilation rate, relative growth rate.

INTRODUCTION

A controversy has arisen concerning the effect of herbivory upon plant fitness [Belsky 1986, Proulx and Mazumder 1998]. Many studies show that herbivory has detrimental effect upon plant's growth and reproduction [Mattson and Keddy 1975, Morrow and LaMarche 1978, Marshall 1989, Mihaliak and Lincolon 1989, Welter 1991] while other studies demonstrate beneficial effects [Paize and Whitham 1987, Stratus 1988] and still others demonstrate variable effects [Maschinski and Whitham 1989, Gedge 1992]**.** The contrasting patterns of response have frequently been attributed in grazing intensity [Grime 1973] evolutionary history and plant life-forms [Noy-Meir 1995, Proulx and Mazumder 1998, Osem *et al.* 2002].

Herbivory can be beneficial both at the level of the population and the individual. At the population level for example, herbivory can remove competitors less capable of tolerating or resisting herbivory [Crawley 1989]. At individual level, herbivory can indirectly influence factors external to the plant such as light availability and so affect photosynthesis and consequently, growth. It can also alter photosynthesis directly through changes in source-sink relations and rate of tissue senescence, or through the effects of hormones secreted by herbivores [McNaughton 1984, Senock *et al*. 1991, Hoogesteger and Karlsson 1992].

Depending upon factors such as herbivore body size, mouth-part structure, and within plant variation in food quality, herbivory can result in very different patterns of defoliation. Herbivores may remove tissue in disc like pieces scattered throughout a leaf, or consume either the tip or outer portions of leaf, or entire leaves. All these factors cause variations in photosynthetic capacity and thus growth rate of the plant. Marshall [1989] reported that for two *Sesbania* species, removal of every other leaf vs. removal of half of each leaf could have different consequences. Removal of every other leaf from *S. marcocarpa* has a more damaging effect upon reproduction than does the removal of half of each leaf, but in *S. vesicaria*, total seed mass of seeds per fruit were higher in plants with every leaf removed than with half of each leaf removed. Marquis [1992] demonstrated that the distribution of damage within *Piper arieianum* affected subsequent growth and reproduction. Removal of 10% of the total leaf area scattered throughout the canopy did not significantly reduce seed production, whereas localized damage (10% of total leaf area removed from a single branch) led to diminished growth and seed production at the branch and whole plant level.

Casual field observations with *Abelmoscus esculantus* indicate that both vegetative and reproductive plants are subjected to substantial levels of leaf defoliation. At least five more or less distinct patterns of natural herbivore damage can be observed: (1) half edge, whereby half of the leaf tissue is removed parallel to, but exclusive of the midrib: (2) double edge, partial tissue damage to entire leaf perimeter: (3) perforation, roughly circular portions removed, leaf edges and midrib intact: (4) tip, apex of leaf consumed, often approaching leaf midpoint (Fig.1): and (5) entire leaf defoliation.

In order to test these ideas, we employed a novel experimental approach, in which each pattern of leaf damage was simulated to investigate the interaction between the effects of different defoliation pattern and growth performance of *Abelmoscus esculantus* both within and between the successive time periods. We focused on plant – herbivore processes that occurred at temporal scale in the nature.

MATERIALS AND METHODS

PLANT CULTURE

The seeds of *Abelmoscus eculentus* (L.) were obtained commercially. Seeds of 0.061-0.069g dry weights were chosen and germinated in glass Petri dishes containing distilled water-saturated filter paper. Upon cotyledon emergence, seedlings were transplanted into 1dm^3 pots filled with 1:1 mixture of sand and a peat-based commercial potting soil. Four seedlings were transplanted in to each pot. At the three-leaved stage only one plant was allowed to grow and the others were removed. Plants were grown in glasshouse receiving natural light and photoperiod (April to June). Plants were watered daily and rotated among positions once a week. The experimental protocol was same for all the three experiments.

DEFOLIATION PATTERNS

Experiment 1

This experiment consisted of four defoliation patterns (treatments), four replicates (in randomized block) and four harvests (one weekly). Thirty days after sowing, 64 plants were randomly assigned to each of the following five defoliation treatments: tip, half edge and entire leaf defoliation and un-defoliated controls. Plants were defoliated using scissors as described by Morrison and Reekie [1995], Blundell and Peart [2001].

Each defoliation treatment involved removing approximately half of the total leaf area. Tip defoliation (TD) removed half the length of every leaf on the plant (including the youngest fully emerged leaf, YFEL) starting from the tip. Half edge defoliation (HED) removed half of every leaf on one side parallel to midrib that was left intact. For double edge defoliation (DED), half of the tissue was removed on both sides of every leaf parallel to the midrib that was left intact. The three patterns of tissue removal are depicted in Fig. 1.

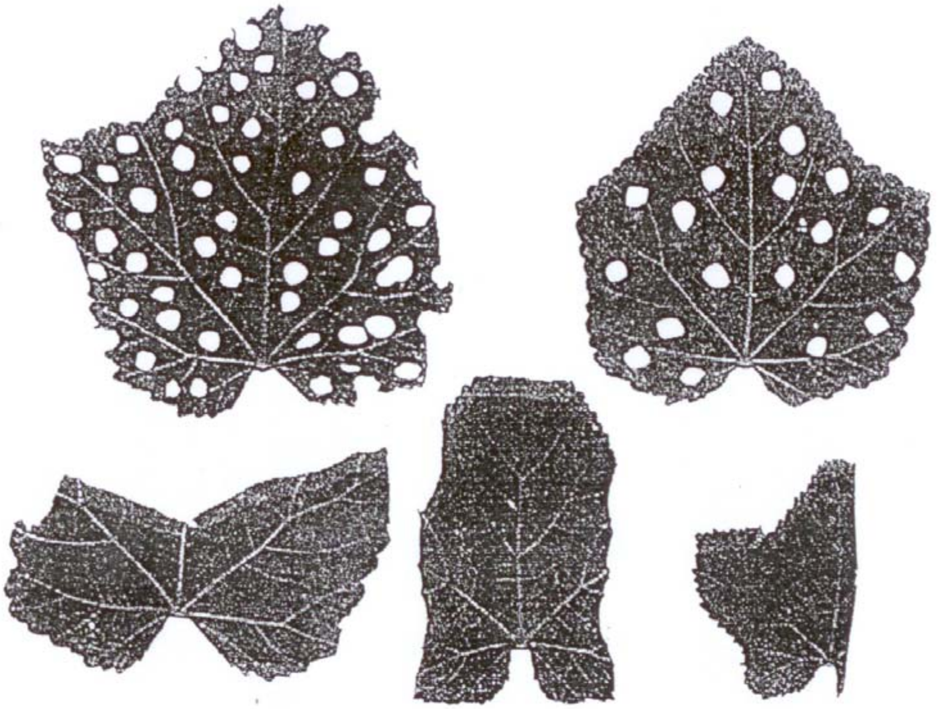

Fig. 1: Various patterns of defoliation: a) Perforation defoliation, b) Tip defoliation, c) Double-edge defoliation and d) half-edge defoliation.

Prior to defoliation, the length and width of each leaf on every plant was recorded. A linear relationship between the leaf area and the product of leaf length x width was derived using detached leaves from the entire leaf defoliation treatment. These data, along with the area of leaf tissue removed, were used to calculate the actual proportion of total plant leaf area removed in each defoliation treatment. Leaf area measurements were made with the automatic Photoelectric Leaf Area Meter (Delta – T devices Ltd.) in high resolution mode.

Experiment 2

This experiment consisted of three defoliation treatments, four weekly harvests and four replicates (in randomize block). After 38 days after sowing, 48 plants assigned to one of the following three treatments: un-defoliated controls, 30% perforation defoliation and 50% perforation defoliation. For perforation defoliation, tissue was punched from within the YFEL leaving the midrib and leaf edges intact (Figs.1a and b). The number of paper-punch perforations (6.0mm in diameter) required to remove approximately 30% and 50% of the leaf area was calculated prior to tissue removal. A clear plastic sheet marked with a grid (about 0.64 cm) was used as describe by Horvitz and Schemske [2002].

Experiment 3

This experiment consisted of four treatments, four replicates (in randomized block) and three harvests. After 45 days of sowing, 48 plants were randomly assigned to one of the following four treatments: un-defoliated controls and low, medium and high leaves of entire leaf defoliation. Leaves were removed beginning with the next to youngest leaf and according to the pattern: low, remove one leaf skips the next two; medium, remove every other leaf; and high, remove two leaves skip the next. In each case therefore, YFEL was left intact. By determining both the amount of leaf area removed and the amount remaining, the exact level of defoliation was calculated as described for experiment 1.

HARVESTING

Plants were harvested on days 1, 7, 14 and 21 after defoliation. At each harvest plants were separated into roots, stems, petioles and leaves. Leaf area was measured using automatic photoelectric leaf area meter (Delta – T devices Ltd.). Dry mass values of leaves, stem, roots and petioles were recorded after 48hrs drying at 80°C. Roots had been washed free of soil before drying. The values of dry weight and leaf area were used for further calculation and data analysis.

DATA ANALYSIS

Mass ratios for roots (*RWR*), stem (*SWR*), petioles (*PWR*) and leaves (*LWR*), also specific leaf area (*SLA*, cm^{-2} g^{-1}), leaf area ratio (*LAR*, cm^{-2} g^{-1})

and relative growth rates (*RGR*: day^{-1}), net assimilation rate (*NAR*: g cm^{-2} day^{-1}) were calculated by using Classical Growth Analysis procedure as defined by Causton and Venus [1981]:

Symbol	Description	Units
RGR	Relative growth rate is an increase in dry weight per unit plant dry weight.	d^{-1}
NAR	Net assimilation rate is net gain in dry weight per unit of leaf area	Gcm^{-2}d^{-1}
LAR	Leaf area ratio is the relative amount of biomass, a plant invests in leaf area	cm^{-2}g^{-1}
SLA	Specific leaf area is the quotient of total leaf area of total leaf dry weight.	cm^{-2}g^{-1}
LWR	Leaf weight ratio is the weight of leaf as a proportion of whole plant.	
SWR	Stem weight ratio is the weight of stem as a proportion of whole plant.	
PWR	Petiole weight ratio is the weight of petiole as a proportion of whole plant.	
RWR	Root weight ratio is the weight of roots as a proportion of whole plant.	

The effects of the defoliation patterns on physiological traits including rates of growth and assimilation and ratios of leaf area and biomass allocation to different plant organs were examined by using analysis of variance (GLM-program). The data of each experiment was analyzed separately. Duncan's [1955] least significant difference (LSD) test was used to compare treatment means. Appropriate graphs were drawn, with significant differences indicated by bars of least significant difference, derived from Duncan's [1955] d-tables. The residual sum of squares in the analysis of variance (ANOVA) was used to calculate the LSD.

RESULTS

EXPERIMENT 1

Rates

Defoliation pattern had significantly influenced the assimilation and relative growth rates that can be ranked in order of: tip-defoliation = half edge-defoliation < un-defoliated plants = double edge-defoliation. Un-defoliated plants showed a significant decline followed by a similar rise during the experimental period. These ontogenetic trends were just opposite to those of tip-defoliated plants. Half-edge defoliated (HED) and double edge defoliated (DED) showed similar trends at the onset of the experiment and thereafter, DED exhibited increasing, while HED decreasing trends in their *RGRs* (Fig. 2a). These ontogenetic trends were also true for *NAR* (compare Figs. 2a and 2b). Consequently, the differences among different defoliation treatments appeared at one time became disappeared at the other during the experimental and was thus responsible for the occurrence of significant interaction between harvest (plant age) and treatment (Table 1).

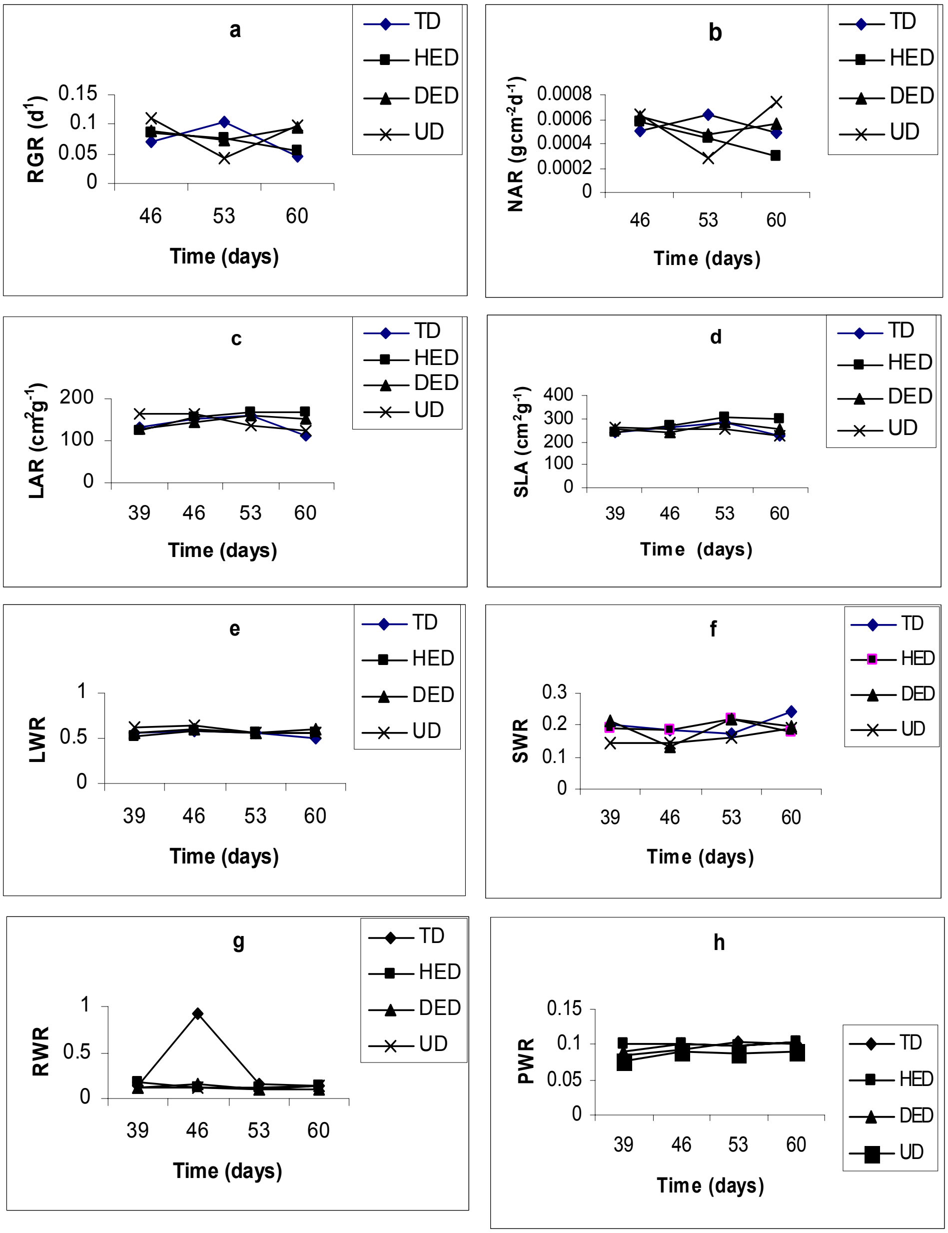

Fig. 2: Responses of RGR (a), NAR (b), LAR (c), SLA (d), LWR (e), SWR (f), RWR (g) and RWR (h) to tip defoliation (TD), half edge defoliation (HED), double edge defoliation (DED) and un-defoliated control (UD) plants of *Abelmoscus esculentus.*

Table 1: Analysis of variance of growth parameters: net assimilation rate (NAR), relative growth rate (RGR), leaf area ratio (LAR), specific leaf area (SLA), leaf weight ratio (LWR), stem weight ratio (SWR), root weight ratio (RWR) and petiole weight ratio (PWR) of *Abelmoscus esculentus* having different defoliation treatments.

Source	NAR	RGR	LAR	SLA	LWR	SWR	RWR	PWR
Experiment 1								
Treatments (T)	4.23**	3.23*	1.92	2.56	3.32*	6.08**	2.11	2.82*
Harvest (H)	8.72**	4.81*	5.36**	3.50*	3.69*	6.19**	1.94	1.76
T * H	13.39***	12.65***	04.58***	1.73	1.62	3.54**	2.32*	0.036
Experiment 2								
Treatments (T)	4.43	3.06	10.54***	3.23*	5.91**	0.056*	4.72*	0.54*
Harvest (H)	6.62**	8.27**	4.61**	1.74	39**	3.34*	3.63*	1.23
T * H	19.87***	19.87***	3.35**	5.98***	5.84***	2.92*	2.64*	2.9*
Experiment 3								
Treatments (T)	8.08**	7.38**	20.8***	2.8*	27.94***	18***	8.44***	1.75
Harvest (H)	13.78**	6.19*	9.94***	6.35**	26.82***	2.48	9.26**	16.3***
T * H	7.94**	04.83**	5.31**	3.69**	2.88*	2.26*	0.096	2.23

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

Ratios

The results (Table 1 and Fig. 2c) suggested that different pattern of defoliation had different impact on the temporal trends of leaf area per unit plant weight. *LAR* of un-defoliated plants showed decreasing, often significant trends during the experiment. On the other hand, half edge and double edge defoliated plants showed increasing trends. These trends were not true for tip-defoliated plants (Fig. 2c). The ontogenetic changes in *LAR* of un-defoliated plants were due to similar changes in *LWR* (Fig. 2e), while that of half edge-defoliated and tip-defoliated plants was largely due to *SLA* (Fig. 2d). In double edge-defoliated plants both *SLA* and *LWR* contribute equally in determining the ontogenetic changes in *LAR*. Beside differences in ontogenetic trends, no marked differences in mean values of either *LAR* or its components (*SLA* and *LWR*) were found among different defoliation patterns.

Table 2: Mean values of net assimilation rate (NAR, g cm $^{-2}$ d^{-1}), relative growth rate (RGR, d^{-1}), leaf area ratio (LAR, cm^{-2} g^{-1}), specific leaf area (SLA, cm^{-2} g^{-1}), leaf weight ratio (LWR), stem weight ratio (SWR), root weight ratio (RWR) and petiole weight ratio (PWR) of *Abelmoscus esculentus* having different defoliation treatments: Tip-defoliation (TD), half edge-defoliation (HED), double edge-defoliation (DED), un-defoliate (UD), 30% perforation-defoliation (PD1), 50% perforation (PD2) low entire defoliation (LED), medium entire defoliation (MED) and high entire defoliation (HED)

Exp. No.	Treatments	NAR	RGR	LAR	SLA	LWR	SWR	RWR	PWR
1	TD	0.00049	0.0731	138.94	251.65	0.5581	0.199	0.133	0.095
	HED	0.000438	0.0726	153.57	276.70	0.5539	0.194	0.139	0.10
	DED	0.000552	0.0858	145.70	257.35	0.5820	0.189	0.114	0.98
	UD	0.000548	0.083	139.10	248.40	0.5930	0.160	0.119	0.086
2	PD1	0.00049	0.064	139.97	263.41	0.5268	0.1823	0.125	0.064
	PD1	0.000332	0.048	135.16	246.70	0.5286	0.182	0.166	0.0671
	UD	0.00034	0.0501	166.46	295.36	0.5629	0.184	0.139	0.069
3	LED	0.000465	0.0456	125.49	263.25	0.4492	0.206	0.161	0.063
	MED	0.000411	0.049	121.69	270.65	0.4441	0.246	0.1738	0.078
	HED	0.00076	0.077	104.26	299.87	0.4001	0.247	0.202	0.073
	UD	0.00032	0.0543	169.58	301.19	0.5654	0.172	0.131	0.068

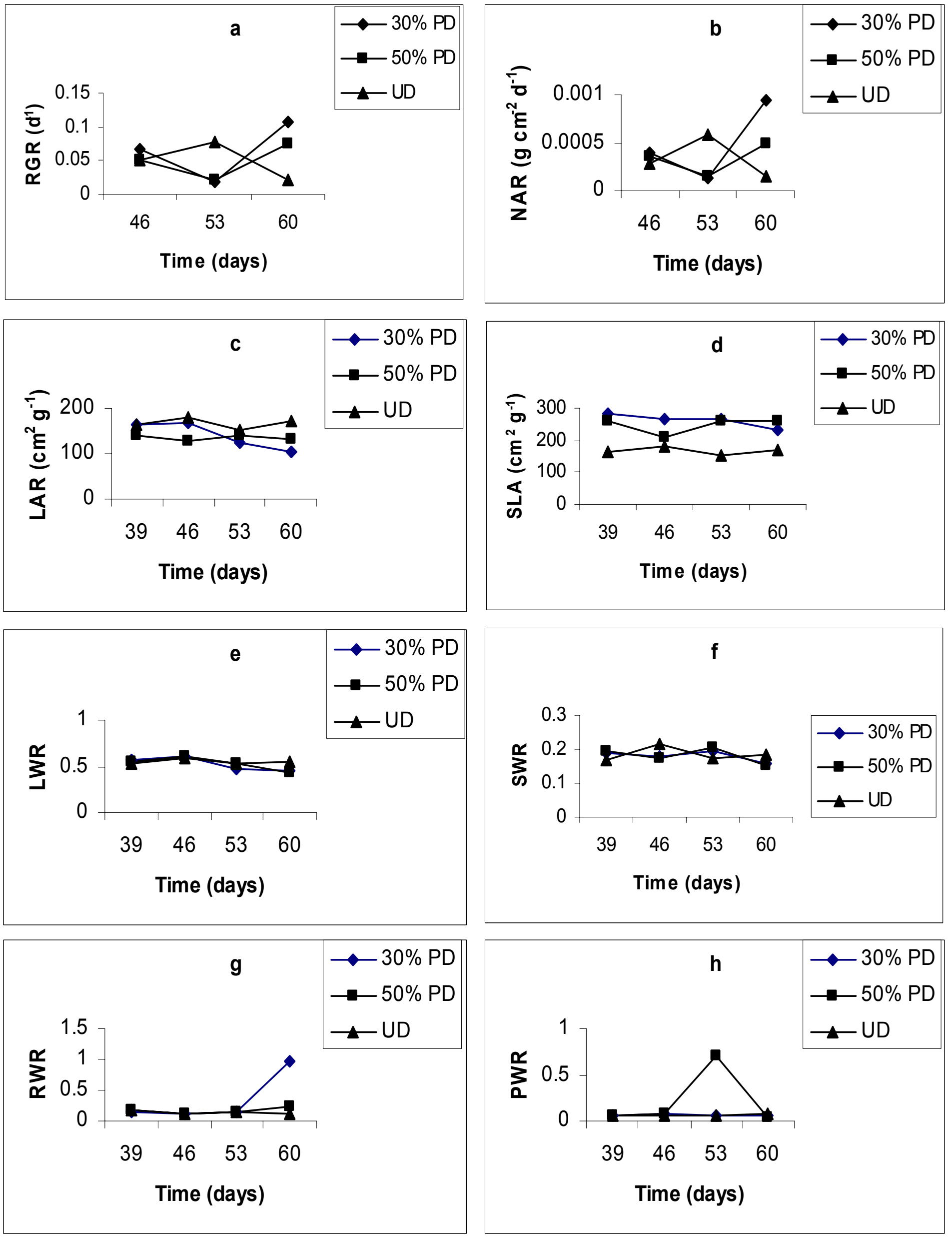

Fig. 3: Responses of RGR (a), NAR (b), LAR (c), SLA (d), LWR (e), SWR (f), RWR (g) and RWR (h) to 30% tip defoliation (TD), half edge defoliation (30% PD), 50% perforation defoliation (PD) and un-defoliated control (UD) plants of *Abelmoscus esculentus.*

In response to defoliation often significant shifting in biomass from leaves to stems, roots, and petioles were observed (Table 2). However, the magnitude of shifting to these organs was specific for specific pattern of defoliation during the experiment (Fig. 2f-2h). Generally, ontogenetic decreases in *LWR* or *RWR* (2h) were often linked with similar increases in *SWR* (Fig. 2f). This pattern of biomass allocation was true for double edge-defoliation.

EXPERIMENT 2

Rates

Although the main effect of defoliation was not significant, the significant interaction between harvest and defoliation levels (Table 1) suggested the differential ontogenetic responses of plant having different perforation-defoliation levels. Un-defoliated plants exhibited a significant rise followed by a similar decline in their *RGR* during the experimental period (Fig. 3a). These ontogenetic trends in *RGR* were almost reverse to those found in defoliated plants. However, no significant difference in ontogenetic trends among 30% and 50% perforation-defoliation levels were observed during the experiment. The ontogenetic changes in *NAR* showed by defoliated and un-defoliated plants were mirrored the changes observed in their *RGRs* (Fig. 3b). Among the perforation-defoliation treatments, 30% promoted the *NAR* while no significant difference between 50% and un-defoliated control plants were found (Table 2).

Ratios

Defoliation reduced all the leaf attributes (*LAR, SLA* and *LWR*) regardless of the pattern of leaf removal (Tables 1 and 2). The 30% perforation-defoliation led to a steady decrease in *LAR*, while 50% removal of tissues caused very little variations in *LAR* during the experimental period (Fig. 3c). These changes in *LAR* were largely due to similar changes in *SLA* (Fig. 3d) rather than *LWR* (Fig. 3e).

There were little differences in biomass allocation to stems and petioles among the treatments. Initially all the experimental treatments exhibited similar values but 50% perforation-defoliation treatment stimulated the allocation to the roots during the last week of experimental period (Fig.3h). This increase in biomass allocation to roots was partly due to decrease in SWR (Fig. 3f) and largely due to PWR (Fig. 3h).

EXPERIMENT 3

Rates

Significant differences in *RGR* between different levels of defoliations were found (Tables 1 and 2). High defoliation resulted into high *RGR* while, no significant differences were found between un-defoliated plants and the plants receiving low or medium defoliation treatments. Plants having high defoliation level exhibited significantly higher *RGR* than the un-defoliated control plants and all other defoliation treatments at the onset of the experiment (Fig. 4a). Thereafter, Plants receiving high defoliation treatment showed a steady often significant decline and their *RGRs* reached to a level not significantly different from the plants exposed to other defoliation treatments. The *RGR* of un-defoliated plants and plants having either low or medium defoliation treatments remained stable during the experimental period. The ontogenetic trends described for *RGRs* of different defoliation treatments were also true for their *NARs* (Fig. 4b).

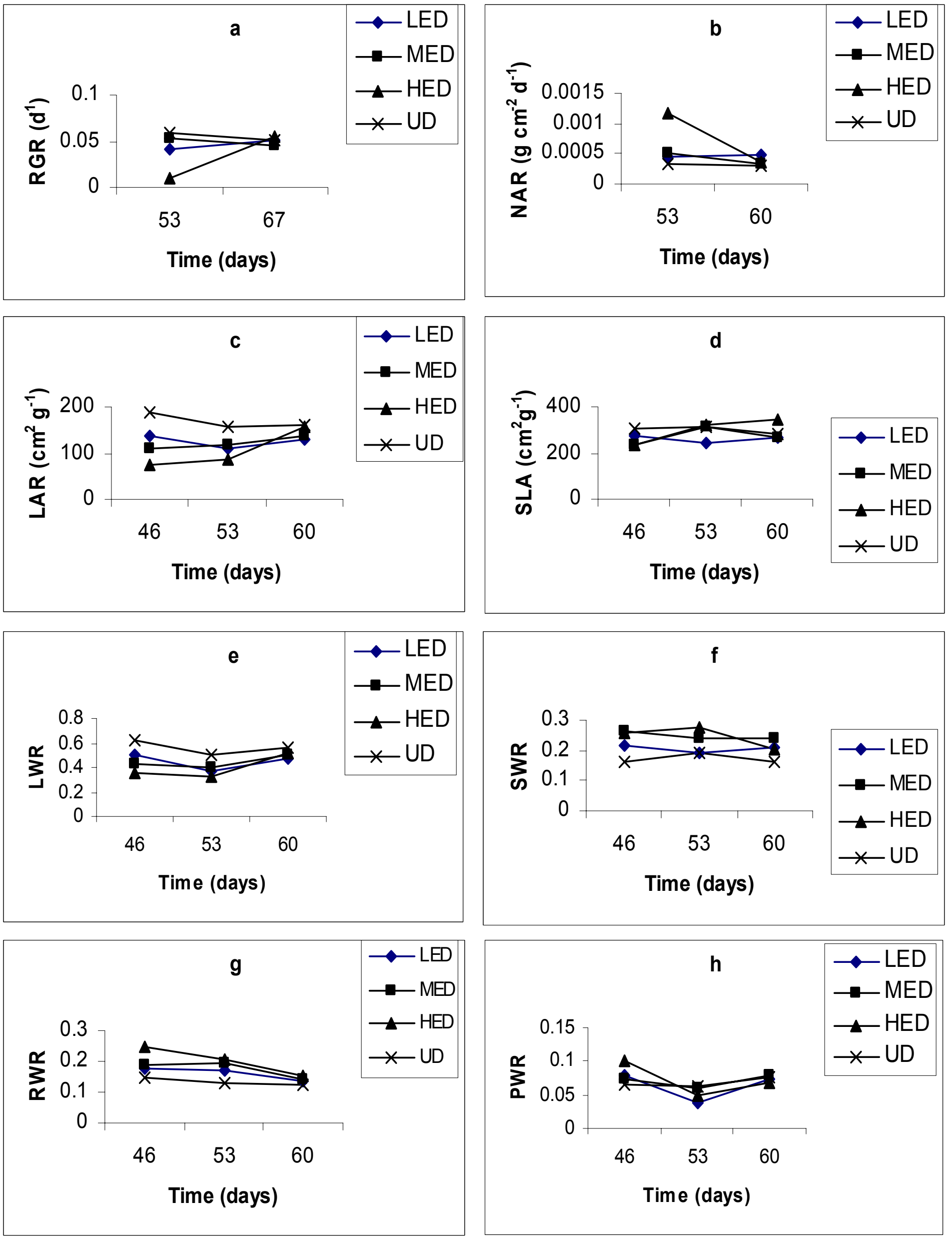

Fig. 4: Responses of RGR (a), NAR (b), LAR (c), SLA (d), LWR (e), SWR (f), RWR (g) and RWR (h) to low defoliation (LED), medium defoliation (MED), high defoliation (HED) and un-defoliated control (UD) plants of *Abelmoscus esculentus.*

Ratios

All the leaf attributes (*LAR, SLA, LWR*) decreased in response to defoliation regardless of the pattern of leaf removal (Table 1) During the first week after defoliation, *LAR* of control plants was higher than all other defoliation treatments. During the second week of post defoliation, plants receiving high defoliation treatment (75%) exhibited a significant rise and approaches to a level not significantly different from the *LAR* of control plants (Fig. 4c). Comparable ontogenetic changes were observed in both components of *LAR*: *SLA* (Fig. 4d) and *LWR* (Fig. 4e).

Defoliation promoted the biomass allocation to stem (*SWR*), roots (*RWR*) regardless of defoliation patterns. The ontogenetic responses of biomass allocation to defoliation patterns were comparable in both stem and root. The significant interaction between harvest and treatment (Table 1) and again the results depicted in Fig. 2f suggested that the differences in *SWR* between defoliation treatments appear at one time became disappeared at the other time during the experimental period.

DISCUSSION

The most striking result of this study was that defoliated plants compensated for the 50% loss of the photosynthetic tissues and maintained growth rate at a level similar to un-defoliated plants. However, the magnitude of compensation was specific for specific pattern of defoliation. Most of the defoliation pattern even leads to increased growth rate (i.e. overcompensation) as predicted by McNaughton [1983]. The compensation response obtained in this study indicates that plants were well able to tolerate the defoliation levels used in our experiment. The increased growth rate observed in response to certain defoliation patterns may be considered as an adaptation against herbivory [McNaughton 1985, Sharifi *et al*. 1987, Dyer *et al*. 1993, Milchunas and Lauenroth 1993, Dyer *et al*, 1995]. Although the direct loss of photosynthetically active tissue implies a reduction in fitness, the plants may, in the long term, respond to damage by activation of meristems, intensification of cell division and delay of senescence, which together result in compensatory growth [Horvitz and Schemske 2002].

As the growth rate is regulated by two primary factors: the efficiency of the leaves and ratio of leaf biomass to whole plant biomass [Causton and Venous 1981], further analysis of these parameters is imperative. The results of the present investigation suggested that *NAR* is the major determinant of the responses of relative growth rate to different defoliation patterns during the experiment. The removal of some leaves or part of leaves results in stimulation in the photosynthetic activity of the remaining leaves (Table 2). This may involves an increase in carboxylating efficiency, presumably due to an increased supply of nutrients or hormones to the surviving leaves. This process therefore results in a compensation for the lost tissue [Crawley 1989, Morrison and Reekie 1995].

The results of this study demonstrate that certain defoliation treatments enhanced *NAR* (over-compensation) of residual tissue, while others slightly depress it relative to controls. These differences can be seen most clearly in experiment 3 (Table 2). These responses illustrate that the way in which tissue is removed can have a dramatic effect upon photosynthetic capacity of the remaining tissue. These results are in accord with those of Morrison and Reekie [1995].

It is important to note that the age of the plants (days of post germination) varied among experiments. In accordance with this, control net assimilation rate and growth rates also varied among experiments in that younger plants had higher net assimilation rate than those plants used at a later date. An ontogenetic decrease in assimilative capacity is not new and is common phenomenon in higher plants [Crawley 1989, Dasti 1994]. The leaves of most plants go through a predictable change in their photosynthetic capacity as they age. Several factors may contribute to the observed ontogenetic decline in the net assimilation rate. One likely explanation is that the maintenance and growth components of respiration increased with increased plant age [Dasti 1994].

The net photosynthesis of entire leaf canopies can be conveniently described in terms of *LAR*; this is the area of photosynthetic surface per unit of plant weight. We often found an inverse relationship between *LAR* and *NAR*. This might be expected because at very high *LAR* much photosynthate is potentially wasted in respiration of shaded leaves. The removal of physiological sinks, such as developing leaves, and sources, such as mature leaves, generally induce different, sometimes contrasting, plant responses [Haukioja and Honkanen 1996, Zvereva and Kozlov 2001]. Certain defoliation treatments (i.e. tip-defoliation, half edge-defoliation and double edge-defoliation) enhanced *LAR*, while others (i.e. perforation-defoliation, low entire-defoliation, medium entire-defoliation and high entire-defoliation) decreased *LAR* relative to controls. These dramatic differences in the effect of defoliation patterns on *LAR* appear to be related in part, to differences in the amount of leaf area constructed per unit leaf weight (*SLA*).

BIOMASS ALLOCATION

Herbivory can alter the sink-source relations and consequently pattern of internal allocation of resources between below ground growth parameters as well as above ground ones [Evans 1991, Hulme 1996]. Removal of leaves has two main consequences: (1) the remaining leaves show large increase in photosynthetic rate [Maggs 1965, Hodginson 1974] as a result of the increased sink strength or developing leaves. (2) Sink strength of roots is reduced relative to these new leaves and roots may actually become a carbon source [Bokhari 1977]. After defoliation, initially biomass shift from *LWR* towards *RWR* and SWR, however with the passage of time defoliated plants undergo compensatory shoot and root growth. This finding agrees with the observations of Ennik [1966], Evans [1971]. Initial shifts of biomass towards roots and shoots, was observed in tip, half edge, double edge, low entire, medium entire, high entire defoliated plant. On the other hand 30% and 50% perforation defoliated plant do not show any variations in *SWR* and *RWR* with correspondence to control. However, at the end of experiment 50% perforation-defoliated plants showed a tremendous increase in *RWR*. In overall analysis of biomass allocation in all the three experiments it was clearly observed that defoliated plants undergo compensatory growth with the passage of time.

References

Belsky, A.J. (**1986**) “Does herbivory benefits plants? A review of the evidence”, *American Naturalist*, 127, 870-892.

Blundell, A.G. and Peart, D.R. (**2001**) “Growth strategies of shade-tolerant tropical tree: the interactive effects of canopy gaps and simulated herbivory”, *Journal of Ecology*, 89, 608-615.

Bokhari, V.H. (**1977**) “Regrowth of western wheatgrass utilizing C-labelled assimilates stored in belowground parts”, *Plant and Soil*, 48, 115-127.

Causton, D.R. and Venous, J.C. (**1981**) “The Biometry of Plant Growth”, Edward Arnold.

Crawley, M.J. (**1989**) “Insect herbivores and plant population dynamics”, *Annual Review of Entomology,* 34, 531-564.

Dasti, A.A. (**1994**) “Physiological responses to water stress in some subtropical arid zone grasses”, PhD Thesis, Univ. Wales, Aberystwyth

Duncan, B.D. (**1955**) “Multiple-range test d-tables”, *Biometrics*, 11, 1-42.

Dyer, M.I. Moon, AM. Brown, M.R. and Crossley (**1995**) “Grasshopper crop and midgut extract effects on plants, an example of reward feedback”, *Proc. of the National Academy of Science* (USA), 92, 5475-5478.

Dyer, M.T., Turner, C.L. and Seastedt, T.R. (**1993**) “Herbivory and its consequences”, *Ecological Applications,* 3, 10-16.

Ennik, G.C. (**1966**) “Influence of Clipping and Soil Fumigation on Shoot and Root Production of Perennial Rye Grass and White Clover”, Jaarbock der Institute biology Schiek Onderg Landb Grewass, p.11.

Evans, A.S. (**1991**) “Whole plant responses of *Brassica campestris* (Cruciferae) to altered sink-source relations”, *American Journal of Botany*, 78, 394-400.

Evans, P.S. (**1971**) “Root growth of *Lolium perenne* L. II. Effects of defoliation and shading”, *Newzealand Journal of Agricultural Research*, 14, 552-562.

Gedge, K.E. (**1992**) “Effects of herbivory on two Great Lakes beach annuals; *Cakile edentula* and *Corispermum hyssopifolium*”, M.Sc. Thesis, Department of Plant Science, University of Western Ontario.

Grime, J.P. (**1973**) “Competitive exclusion in herbaceous vegetation”, *Nature*, 242, 344-347.

Hall, I.V. Steiner, E. Threadgill, P. and Jones, R.W. (**1988**) “The biology of Canadian weeds. 84. *Oenothera biennis* L.”, *Canadian Journal of Plant Science*, 68, 163-173.

Hawkijoa, E. and Honkanen, T. (**1996**) “Why are tree and responses to herbivory so variable? Dynamics of forest herbivory: Quest for pattern and principle”, W.J. Mattson, P. Niemela and M. Rousi (Eds.), *U.S. Forest Service General Technical Report Nc-183*, U.S. Forest service Minneapolis, pp. 1-10.

Hodginson, KC. (**1974**) “Influence of partial defoliation on photosynthesis and transpiration by Lucerne leaves of different ages”, *Acitralian Journal of Plant Physiology*, 1, 561-578.

Hoogesteger, J. and Karlsson, P.S. (**1992**) “Effects of defoliation on radial stem growth and photosynthesis in the mountain birch *Betula pubescns* ssp. Tortuosa)”, *Functional Ecology*, 6, 317-323.

Horvitz, C.C and Schemske, W.D. (**2002**) “Effect of plant size, leaf herbivory, local competition and fruit production on survival, growth and future reproduction of a neotropical herb”, *Journal of Ecology*, 90, 279-290.

Hulme, P.E. (**1996**) “Herbivores and performance of grassland plan: a comparison of arthropod, mollusk, and rodent herbivory”, *Journal of Ecology*, 84, 43-51.

Maggs, D.H. (**1965**) “Growth rates in relation to assimilate supply and demand II. The effect of particular leaves and growing regions in determining dry matter distribution in young apple trees”, *Journal of Experimental Botany*, 16, 387-404.

Marquis, R.J. (**1992**) “A bite is a bite? Constraints on response to folivarry in *Piper arieianum* (Piperaceae)”, *Ecology*, 73, 143-152.

Marshall, D.L. (**1989**) “Intergration of response to defoliation within plants of two species of *Sesbani*”, *Functional Ecology*, 3, 207-214.

Maschinski, J. and Whitham, T.G. (**1989**) “The continuum of plant responses to herbivory: the influence of plant association, nutrient availability, and timing”, *American Naturalist*, 134, 1-19.

Mattson, W.J. and N.D. Keddy (**1975**) “Phytophagous insects as regulators of forest primary production”, *Science*, 190, 515-521.

McNaughton, S.J. (**1983**) “Compensatory plant growth as a response to herbivory”, *Oikos*, 40, 329-336.

McNaughton, S.J. (**1984**) “Physiological and Ecological Implications of Herbivory. Encyclopedia of Plant Physiology”, Springer-Verlag, Berlin, p. 657.

McNaughton, S.J. (**1985**) "Interactive regulation of grass yield and chemical properties by defoliation, a salivary chemical, and inorganic nutrition", *Oecologia*, 65, 478-486.

Mihaliak, C.A. and Lincolon, D.E. (**1989**) "Plant biomass partitioning and chemical defense: response to defoliation and nitrate limitation", *Oecologia*, 80, 122-126.

Morrison, K.D. and Reekie, G.E. (**1995**) "Pattern of defoliation and its effects on photosynthetic capacity in *Oenthra biennis*", *Journal of Ecology*, 83, 759-761.

Morrow, P.A. and LaMarche, V.C. (**1978**) "Tree ring evidence for chronic insect suppression of productivity in sub-alpine", *Eucalyptus. Science*, 201, 1244-1246.

Noy-Meir, 1. (**1995**) "Interactive effects of fire and grazing on structure and diversity of Mediterranean grasslands", *Journal of Vegetation Science*, 6, 701-710.

Osem, Y., Perevolotsky and Kigel, J. (**2002**) "Grazing effect on diversity of annual plant communities in a semi-arid rangeland: interactions with small-scale spatial and temporal variation in primary productivity", *Journal of Ecology,* 90, 936-946.

Paize, K.N. and Whitham, T.G. (**1987**) "Overcompensation in response to mammalian herbivory: the advantage of being eaten", *American Naturalist*, 129, 407-416.

Proulx, M. and Mazumder, A. (**1998**) "Reversal of grazing impact on plant species in nutrient-poor vs. nutrient rich ecosystems", *Ecology*, 79, 2581-2592.

Scheidel, U. and Bruelheide, H. (**1999**) "Selective slug grazing on montane meadow plants", *Journal of Ecology*, 87, 828-838.

Senock, R.S. Sisson W.B. and Donart, G.B. (**1991**) "Compensatory photosynthesis of *Sporobolus fiexuosus* (Thrub) Rydb. Following simulated herbivory in the northern Chihuahuan Desert", *Botanical Grazette*, 152, 275-281.

Sharifi, M.R. Nilsen, E.T. and Rundel, P.W. (**1987**) "Biomass and net primary production of *Prosopis glandulosa* (Fabaceae) in the Sonoran desert of California", *American Journal of Botany,* 69, 760-767.

Stratus, S.Y. (**1988**) "Determining the effects of herbivory using naturally damaged plants", *Ecology,* 69, 1628-1630.

Welter, S.C. (**1991**) "Responses of tomato simulated and real herbivory by tobacco hornworm (Lepidoptera: Sphingidae)", *Environmental Entomology*, 20, 1537-1541.

Zvereva, E.L. and Kozlov, M.V. (**2001**) "Effect of pollution induced habitat disturbance on the response of willows to simulated herbivory", *Journal of Ecology*, 89, 21-30.