VOL. 7, NO. 10, OCTOBER 2012 ISSN 1990-6145
ARPN Journal of Agricultural and Biological Science

www.arpnjournals.com

ECO-PHYSIOLOGICAL TRAITS NAR AND LAR ROLE IN DETERMINING THE RELATIVE GROWTH RATE IN COMPETITION

Allah Bakhsh Gulshan[1, 2], Altaf Ahmad Dasti[2] and Shazia Shakoor[2]
[1]Department of Botany, Government Postgraduate College, Dera Ghazi Khan, Punjab, Pakistan
[2]Institute of Pure and Applied Biology, B.Z. University, Multan, Punjab, Pakistan
E-Mail: abgulshan@hotmail.com

ABSTRACT

Crop responses to weed competition are difficult to predict, particularly in crop production systems. Subsequently models can be used to integrate and to assess the relative importance of the multiple influences on competition. In the present studies the dynamics of competition between grass and different weed species. Two experiments were performed. Experiment #1 was performed to evaluate the variation in growth rates and biomass allocation among the weed flora grown under normal conditions. Experiment # 2 was performed to measure the responses of a particular weed species to competition in natural and agro-ecosystem. NAR and LAR are important factors in determining the RGR of ten herbaceous weed species in combination with grass. The competition was reduced the growth of weed species and effect positively on the grass species. Allocation of physiological traits such as NAR and LAR were more significant for determining the relative growth of different species in competition with grass.

Keywords: weed competition, classical growth analysis, RGR, net assimilation rate, LAR.

INTRODUCTION

In recent plant physiology, much emphasis has been placed on the development of simple, empirically derived classical models that equate eventual crop yield loss with some measurable characteristics of a weed population early in the growing season. Typically, descriptive models of crop weed-competition are valid only for the conditions from which they were developed (Weaver, 1996). In addition to the impact of growing season weather factors that influence the interactions between specific crops and weed combinations include crop and weed densities, relative times of emergence and edaphic characteristics (Firbank *et al.*, 1990; Kropff and Spitters, 1991; Wilson *et al*., 1995).

Plant growth analysis is an explanatory, holistic and integrative approach to interpreting plant form and function. It uses simple primary data in the form of weights, areas, volumes and contents of plant components to investigate processes within and involving the whole plant (Evans, 1972; Causton and Venus, 1981; Hunt, 1990). Hoffmann and Poorter (2002) reported that 28 articles since 1993 have drawn upon the approach in one way or another. We took the simplest possible approach, calculating the most fundamental of the growth parameters according to purely 'classical' methods across one harvest-interval.

Crop-weed models incorporating competition have had considerable success in describing how the process of competition affects crop yield and how strategic weed management decisions impact on weed numbers for a limited range of economically important species. There is, however, a need to increase our understanding of the spatial and temporal variability in model parameters if they are to be used more in a predictive context and to pull together data for a wide range of weeds and crops.

Growth analysis is only one of the many approaches, which provide an opportunity to investigate several interlinked physiological traits and their interactions to the given environment simultaneously. It was commonly accepted that utilization of such interlinked plant traits across several species may have considerable predictive power (Keddy, 1992; Poorter and Remkes, 1990; Nieman *et al*., 1992; Ven de Werst *et al*., 1993). Pandy *et al.* (1980) studied LA, NAR, RGR, CGR, LAR and SLW in found *Vigna mungo* cultivars and reported that leaf area increased till 20 days after sowing in all cultivars. There was an increase relationship between leaf area and NAR. The increase in CGR was ascribed to the increased in NAR and leaf area. Reich *et al*. (1992) using data from diverse sources, life forms and biomes, demonstrated a positive relationship between seedling mean RGR and LAR. Huante *et al*. (1995) were comparing woody seedling form a neo tropical deciduous forest, found mean RGR to correspond with LAR rather than ULR. In other findings, he reported the mean RGR of woody species from a geotropically deciduous forest corresponded both with SLA and with LWR.

Relative growth rate (RGR) differences between native and invasive plant species is widely thought to be a major factor contributing to invasion, particularly following disturbance (Baker, 1974; Grime and Hunt 1975). RGR is a complex parameter determined by a number of physiological, morphological and biomass-allocation components. Much research has centered on describing RGR differences between native and invasive species (Baskin *et al.*, 1999; Bellingham *et al*., 2004; Burns, 2004). Less is known, however, about the underlying mechanisms driving RGR differences between native and invasive species. Such understanding is critical for effective management of current invaders and prediction and management of future invaders. Native species adapted to the nutrient-poor soils of arid and semiarid rangelands often exhibit a lower RGR than their invasive counterparts (Cronk and Fuller, 1995; Pattison *et* *al*., 1998; Garcia-Serrano *et al*., 2005), and the magnitude of these differences often intensifies with increased resource availability (Daehler, 2003). A high RGR allows invasive to rapidly occupy space and capture resources and reduces the time between vegetative growth and reproduction (Poorter, 1989). The advantages of low RGR demonstrated by native species, however, are less clear, causing some researchers to suggest that natural selection in nutrient-poor environments has targeted one of the underlying components of RGR instead of RGR itself (Lambers and Dijkstra, 63.1987). For example, traits allowing conservation and efficient use of resources may be advantageous in resource-poor systems, but these traits also may lower RGR. In turn, these traits may not be advantageous following disturbance when resource availability increases. Plant growth analysis decomposes RGR into net assimilation rate (NAR, rate of dry matter production per unit leaf area) and leaf area ratio (LAR, leaf area per unit total plant mass), where RGR=NAR x LAR (Evans, 1972; Causton and Venus 1981). NAR is determined primarily by the ratio of carbon gained through photosynthesis and carbon lost through respiration. LAR reflects the amount of leaf area a plant develops per unit total plant mass and, therefore, depends on the proportion of biomass allocated to leaves relative to total plant mass (leaf mass ratio, LMR) and how much leaf area a plant develops per unit leaf biomass (specific leaf area, SLA), where LAR = LMR x SLA.

Most work evaluating RGR variation among species has compared species from habitats differing in fertility or productivity. Early studies demonstrated that the higher RGR achieved by species from fertile habitats was a result of differences in LAR and SLA between species (Poorter and Remkes, 1990). Later experiments and recent meta-analysis attribute these differences to 81.variation in NAR, not LAR or SLA (Villar *et al*., 2005; Shipley, 2006). Other studies have found that both NAR and SLA contribute significantly to differences in RGR among species (Grotkopp *et al*., 2002). These variable results suggest that a number of mechanisms could drive RGR differences between native and invasive species. Invasive could achieve higher RGR than natives by having higher rates of photosynthesis and/or lower rates of respiration (high NAR), allocating more biomass to leaves (high LMR), or producing thinner or less dense leaves resulting in more leaf area per unit leaf biomass (high SLA). Only a few studies have evaluated the underlying causes of RGR variation between native and invasive species. In the Great Basin, invasive annual grasses generally have greater LAR and SLA but not NAR than bunchgrasses (Arredondo *et al*., 1998). However, annual grasses, in general, tend to have lower LAR and SLA than perennials, so it is not necessarily clear that these traits were unique to invaders in this system (Garnier, 1992). In a comparison of invasive and noninvasive Pinus species, differences in NAR, LMR, and SLA all contributed to variation in RGR, but SLA was the main factor allowing invasive to achieve a higher RGR than noninvasive pines (Grotkopp 99. *et al*., 2002). Together, these studies suggest SLA may be a key factor driving RGR differences between native and invasive plants. In support, high SLA has been correlated to invasion success at both the community and the continental scale (Lake and Leishman, 2004; Hamilton *et al*., 2005). Producing more leaf area per unit biomass may provide a greater overall return on carbon investment, allowing invasive plants to achieve higher RGR than natives. James and Drenovsky (2007) determined the mechanistic basis for RGR differences between native and invasive forbs that are widely established on the nutrient-poor soils of the Intermountain West. Path analysis was used to identify the physiological and morphological components of RGR that drive RGR differences between native and invasive species. We predicted that greater SLA would be the key factor allowing invasive to achieve a higher RGR than natives.

The purpose of the present study was investigate through using a range of ten herbaceous dicotyledonous weed plant species and several ecophysiological traits measured for each of the species, the degree to which the various types of interactions have potential for predicting outcomes of interactions involving plant species. The ultimate goal was to evaluate whether predictive comparative approaches could assist with the generation of general principles about how ecophysiological traits may contribute to the performance and effects of plant at the ecosystem level of resolution.

In addition, the studies of dynamics competition between grass *Echinochloa crus-galli* L. and different weed species *Anagallis arvensis* L., *Chenopodium album* L., *Chenopodium murale* L., *Conyza bonariensis* L., *Coronopus didymus* L., *Eclipta prostrata* L., *Malva neglecta* Wallr., *Melilotus albus* Desr., *Rumex dentatus* L. and *Solanum nigrum* L. were studied in order to determine: How ecophysiological traits may contribute to the performance and effects of plant at different growth levels and the critical phases of grass *Echinochloa crus-galli* L. development as affected by the weeds.

MATERIALS AND METHODS

Experimental design

The pot experiment consisted of two treatments of competition (competition^{+ve} and competition^{-ve}), three harvests and four replicates and all the pots were arranged in completely randomized block design. This arrangement provided the following four combinations:

Dicotyledonous herbaceous in monoculture
Dicotyledonous herbaceous in combination (Mixture)
Monocotyledon grass (*Echinochloa crus-galli* L.) in monoculture
Monocotyledon grass (*Echinochloa crus-galli* L.) in combination

In each block three pots were set up for each species in combination with *Echinochloa crus-galli* L. for evaluation of competitive interaction. Each pot consisted of one herbaceous plant in the center, and three *Echinochloa crus-galli* L. plants each positioned about

4cm from the herbaceous plant in a radial pattern. Thirty pots were also established per block with three grasses per pot but without the herbaceous species, to serve as monocultures for competition experiments. The densities and proportions of plant species were used for investigating competition between herbaceous plants and grass most closely resemble those found in the field and have previously been shown to appropriate for this type of study (Wardle and Nicholson, 1996) to 148.accommodate losses due to plant mortality during the experiment, more pots 149.than the required were set up.

For each dicotyledonous herbaceous species at each of three different developmental stages, one pot per block was destructively harvested for each of the herbaceous dicotyledonous plant monoculture, dicotyledonous plant; *Echinochloa crus-galli* L. combination and *Echinochloa crus-galli* L. monoculture.

Harvested method

The schedule of harvest is given in the Table-1. The first harvest was taken when the plants were 40 days old. Four pots were harvested per species after every ten days and at three developmental stages. At each harvest, plants were separated into roots, stem, leaves and petioles. Roots were washed with water to remove the soil particle. All plant parts were dried at 80˚C for 48hours before recording the dry weights at four-digit balance. Leaf area was measured by leaf area meter.

Table-1 Schedule of planting, harvesting and plant age

Date	Plant age	Activity
1-03-2010	----	Seed sowing
15-03-2010	15	Plant thinning
25-04-2010	25	Harvest I
4-04-2010	35	Harvest II
14-04-2010	45	Harvest III
24-05-2010	55	Harvest IV

The posts containing grass enabled determination of both the competitive effect and response of each of the herbaceous species. At each harvest period for the monoculture, one pot of the herbaceous species + grass combination, and one of the grass monoculture pots, was also destructively for each block; all plants in each pot were clipped off at ground level. The grass material in each pot was oven dried at 80^{o}C for 48 h and the weight of this material was added to the cumulative weight of all the prior trimmings of that pot, to determine the total production of grass during the experiment (Wardle and Nicholoson, 1996). The amount of grass production in the species pots relative to the in the grass monoculture pots, was used as a measure of the net competitive effect of the herbaceous species against grass (Wardle and Nicoloson, 1996). The competitive ability of each species included in the experiment was assessed by its performance (RGR) in monoculture as well in mixture. All the components of RGR and parameters of biomass were evaluated as described for experiment I.

Measurements of eco-physiological traits

Prior to drying, the number of leaves per plant was determined and the leaf area was measured using automatic photoelectric leaf area meter (Delta-T-Device Ltd Bunwell, Cambridge, England). The mean weight of each leaf was also determined. Dry mass values of leaves, stem, roots, petioles, flowers and fruits were recorded after 48 hours drying at 80^{o}C. Roots were washed thoroughly before drying. The values of dry weight and leaf area were used for further calculation of rates and ratios of growth and data analysis.

Data analysis

Relative growth rates (RGR, day^{-1}), Net assimilation rate (NAR, gcm^{-2} day^{-1}), Leaf area ratio (LAR, cm^{-2} g^{-1}) were calculated by using classical growth analysis procedure as defined by Causton and Venus (1981).

Symbol	Units	Description
RGR	d^{-1}	Relative growth rate is an increase in dry weight per unit plant dry weight. (RGR = loge w$_2$- loge w$_1$/ t$_2$-t$_1$)
NAR	gcm^{-2} d^{-1}	Net assimilation rate is net gain in dry weight per unit of leaf area. (NAR = 2(w$_2$-w$_1$)/ (LA$_1$ + LA$_2$) (t$_2$-t$_1$)
LAR	cm^{-2} g^{-1}	Leaf area ratio is the relative amount of biomass, a plant invest in leaf area (LAR = LWR x SLA)

The data of each experiment was analyzed separately using GLM Model of ANOVA. Duncan's (1995), least significant difference (LSD) was also calculated. The residual sum of squares in the analysis of variance (ANOVA) was used to calculate the LSD.

RESULTS

Relative growth rate (RGR) of herbaceous species

The analysis of variance demonstrated that species x treatment and species x harvest were significant in competition. $P < 0.000$ and all other main factors and their interaction were found to be highly significant (Table-2). However the RGR of the plants species *Anagallis arvensis* L., *Coronopus didymus* L., *Eclipta prostrata* L., *Malva neglecta* Wallr, and *Melilotus albus* Desr, in competition was often higher values then the plants which were without competition. While the species *Chenopodium album* L., *Chenopodium murale* L., *Conyza bonariensis* L., *Rumex dentatus* L. and *Solanum nigrum* L. showed lower values of RGR in competition condition. Figure-1 and Table-3 shows that the plants of *Rumex dentatus* L., in mixture exhibits lowest value at the end of the experiment while the plants, which were in monoculture, also showed decreasing trend through out the experiment. However all the plants species showed different response to the treatment? Significant differences in ontogenetic trends were observed in plants exposed to different treatments during the experimental period.

Net assimilation rate (NAR) of herbaceous species

Analysis of variance demonstrated that the species x treatment and species x harvest were highly significantly as $P< 0.000$ (Table-2), as the treatment x harvest main effect was also found to be significant as NAR were influenced with the plant age. In mixture the species *Anagallis arvensis* L., *Coronopus didymus* L. and *Malva neglecta* Wallr, showed high values of NAR as compared to all remaining species. While the NAR of species *Chenopodium album* L., *Chenopodium murale* L., *Conyza bonariensis* L., *Eclipta prostrata* L., *Rumex dentatus* L., and *Solanum nigrum* L., showed negative response to treatment. Result depicted in Figure-2 and Table-5, indicates that the plants of *Malva neglecta* Wallr., in monoculture shows lowest value at the 50 day and it increases at end of the experiment. While the plants of species *Malva neglecta* Wallr, in mixture show increasing trend during the experimental period. The *Rumex dentatus* L., plants in mixture showed negative response to the treatment. The ontogenetic trends exhibited by NAR were those which were found in RGR.

Leaf area ratio (LAR) of herbaceous species

Leaf area ratio was significantly influenced the competition as $P< 0.000$. Much of the variation in LAR was associated with plant age as the harvest main effect was significant $P< 0.000$. LAR increased gradually with increased in plant age. The interaction between the main factors was also found to be significant (Table-2). The plant of *Conyza bonariensis* L. in mixture show high biomass allocation to LAR then the plants, which were in monoculture. While the *Anagallis arvensis* L. and *Melilotus albus* Desr, plants in mixture had lower LAR then the plants in monoculture. Result from Figure-3 and Table-4, indicates that competition had greatly increased the LAR of the *Chenopodium album* L., *Chenopodium murale* L., *Conyza*. *bonariensis* L., *Malva neglecta* Wallr., *Rumex dentatus* L., *Solanum nigrum* Lplants. The species *Anagallis arvensis* L., *Coronopus didymus* L., *Eclipta prostrata* L. and *Melilotus albus* Desr, showed decrease in the LAR values in mixture as compared to monoculture condition (Table-2). The *Anagallis arvensis* L., *Eclipta prostrata* L., *Melilotus albus* Desr., plants in monoculture at day 40 showed highest value of LAR and then it shows decline trend through out the experiment. In contrast *Chenopodium album* L., *Chenopodium murale* L., *Coronopus didymus* L., *Malva neglecta* Wallr., *Solanum nigrum* L., showed lowest value at day 40 and then gradually increase in LAR values at the end of the experiment. These ontogenetic trends were responsible for the significant interaction between species and harvest (Table-2). Thus the LAR of all the plant species were significantly influenced in competition condition (Table-2).

Table-2. Analysis of variance of RGR, NAR and LAR of ten weed species grown under competition.

Source	**Relative growth rate** (d^{-1})				**Net assimilation rate** ($gcm^{-2}d^{-1}$)			**Leaf area ratio** (cm^2g^{-1})		
	DF	**MS**	**F**	**P**	**MS**	**F**	**P**	**MS**	**F**	**P**
Species	9	0.008077	4.97	0.000	1.1471E-06	0.82	0.602	15335	7.63	0.000
Treatment	1	0.004341	2.67	0.105	6.3179E-06	4.49	0.036	4225	2.10	0.149
Harvest	1	0.018954	11.67	0.001	2.8756E-06	2.05	0.155	39682	19.76	0.000
Replicate	3	0.000196	0.12	0.948	3.2723E-06	2.33	0.078	1711	0.85	0.467
Sp*T	9	0.004098	2.52	0.011	2.9080E-06	2.07	0.037	8827	4.39	0.000
SP*H	9	0.009167	5.65	0.000	6.4561E-06	4.59	0.000	95654	2.82	0.000
T*H	1	0.000008	0.01	0.944	2.3780E-06	1.69	0.196	10309	5.13	0.007
Error	126	0.001624			1.4059E-06			2009		
Total	159									

Table-3. Mean values of RGR and NAR for the ten weed species grown in mixture (competition^{+ve}) and grown in monoculture (competition^{-ve}). Values are the averages across four replicates.

Species	**Relative growth rate** (d^{-1})			**Net assimilation rate** (gcm^{-2}d^{-1})		
	Competition^{+ve}	**Competition^{-ve}**	**Mean**	**Competition^{+ve}**	**Competition^{-ve}**	**Mean**
Anagallis arvensis L.	0.014943	-0.00716	0.0038915	0.001108	0.000304	0.000706
Chenopodium album L.	0.008598	0.057486	0.033042	0.000189	0.000601	0.000395
Chenopodium murale L.	0.009463	0.014048	0.0117555	0.000118	0.000985	0.0005515
Conyza bonariensis L.	0.041105	0.103599	0.072352	0.000531	0.000982	0.0007565
Coronopus didymus L.	0.019132	0.002818	0.010975	0.001404	0.000174	0.000789
Eclipta prostrata L.	0.034484	0.024993	0.0297385	0.001138	0.00253	0.001834
Malva neglecta Wallr.	0.020732	0.014938	0.017835	0.000993	-0.000039	0.000477
Melilotus albus Desr.	0.006186	-0.01782	-0.005817	0.0018	0.000096	0.000948
Rumex dentatus L.	-0.00152	0.023488	0.010984	-0.00026	0.000395	0.0000675
Solanum nigrum L.	0.020751	0.060378	0.0405645	0.000283	0.000512	0.0003975
Mean	0.0173874	0.0276768		0.0007304	0.000654	

LSD of Relative growth rate< 0.036 and LSD of Net assimilation rate< 0.0010

Table-4. Mean values of LAR for the ten weed species grown in mixture (competition^{+ve}) and grown in monoculture (competition^{-ve}). Values are the averages across four replicates.

Species	**Leaf area ratio** (cm^{2}g^{-1})		
	Competition^{+ve}	**Competition^{-ve}**	**Mean**
Anagallis arvensis L.	59.88189	124.325	92.103445
Chenopodium album L.	106.4629	85.28281	95.872855
Chenopodium murale L.	130.6631	108.3642	119.51365
Conyza bonariensis L.	161.7733	102.2853	132.0293
Coronopus didymus L.	104.886	113.4443	109.16515
Eclipta prostrata L.	102.1373	120.3972	111.26725
Malva neglecta Wallr.	95.39412	35.31511	65.354615
Melilotus albus Desr.	59.36704	89.50715	74.437095
Rumex dentatus L.	67.48379	53.78917	60.63648
Solanum nigrum L.	128.3672	100.9228	114.645
Mean	101.641664	93.363304	

LSD of Leaf Area Ratio< 40.46

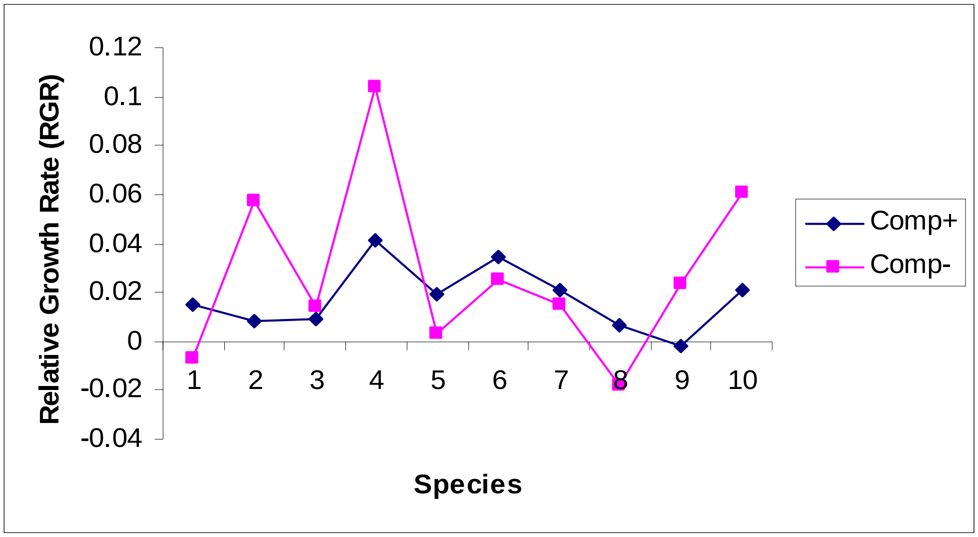

Figure-1. Graphical representation between relative growth rate (d^{-1}) and ten herbaceous species under competition^{+ve} and competition^{-ve} with grass.

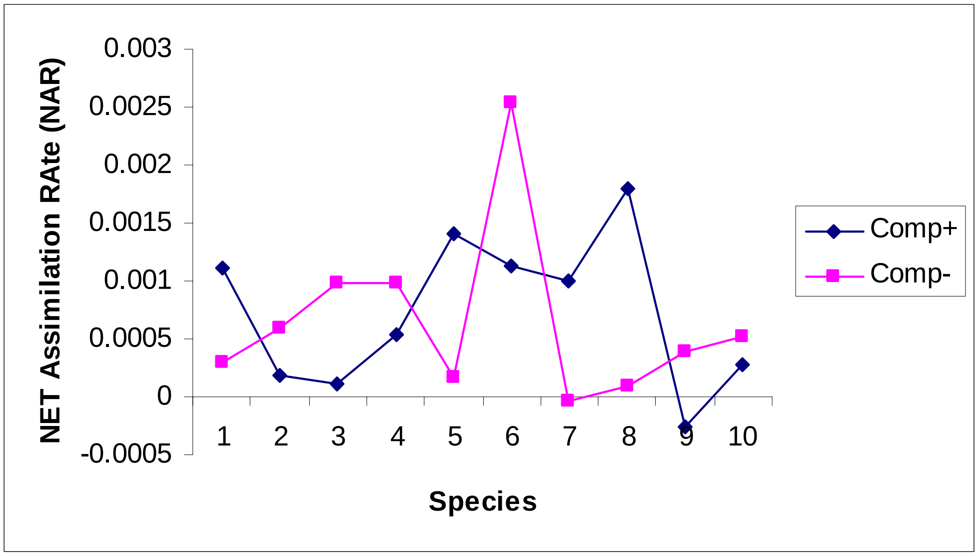

Figure-2. Graphical representation between net assimilation rate (gcm^{-2} d^{-1}) and ten herbaceous species under competition $^{+ve}$ and Competition^{-ve} with grass.

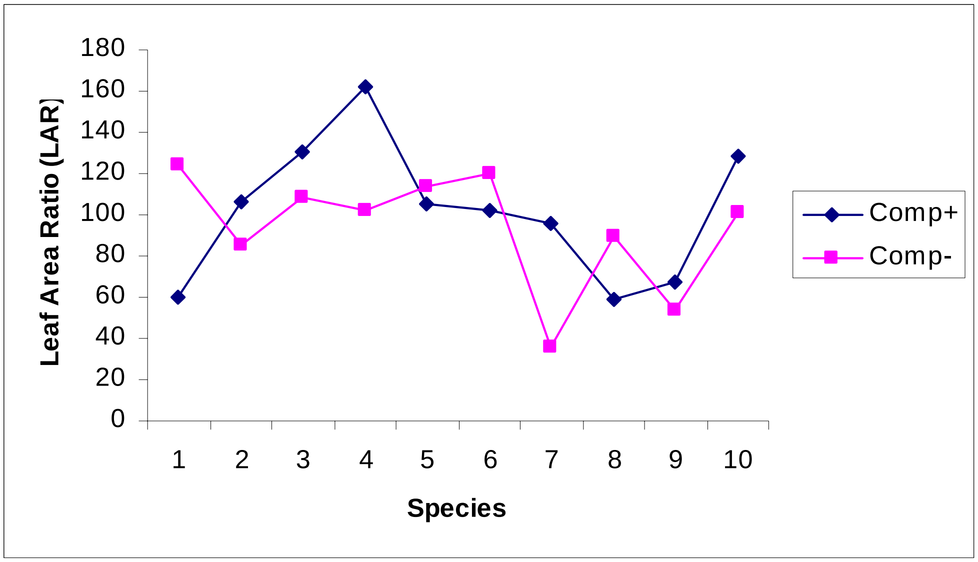

Figure-3. Graphical representation between Leaf Area Ratio (cm^2 g^{-1}) and ten herbaceous species under competition $^{+ve}$ and Competition^{-ve} with grass.

DISCUSSIONS

Results showed that within the plant functional group identified there were large differences between plant species with regard to their traits. Thus there were clear ecophysiological differences between the plant species. The close relationship we found between several of the traits we measured at least partially supports the conclusion of Reich *et al.* (1992) that co variation in several inter linked traits provides a useful conceptual link between process at leaf / whole plant scales, and ecosystem level scales. The suite of ecophysiological traits we measured for each species thus provides a suitable gradient across which biotic interactions and ecosystem level properties can be evaluated.

A close link between Relative Growth Rate and the efficiency of the leaves or the ratio of leaf area to whole plant biomass was found (Causton and Venus, 1981). The relative growth rate of weed species used in the present investigation is determined with NAR and often with LAR. This close association between RGR and NAR is due to a positive relationship between RGR and photosynthetic rate per unit leaf area (Konings, 1989; Garnier, 1992). In climate races of *Dactylis glomerata* (Eagles, 1967) and in *Gneum viburnum* and *Crisum palustre* (Pons, 1977) differences in RGR have been reported to be associated with NAR. Garnier (1992) has compared the RGR of co generic annual and perennial grasses and found the growth differences between two life forms could be described totally to differences in NAR. However the interpretation contradiction the data presented by Brewester and Barnes (1981) and Poorter and Remkes (1990) where the relationship between photosynthetic rate per unit leaf area and RGR was not significant.

The suggestions that interaction between the effects of competition have strong effect on whole plant performance and biomass allocation pattern are supported by the experimental results. The results of the present investigation support the concept of compensatory growth (Richards and Caldwell, 1985), under normal soil conditions competition may increase RGR of grass *Echinochloa crus-galli* (Table-2) while the weed species grown in combination with grass show reduction in RGR (Table-2).

The ecological advantage of high RGR is very clear. Due to high RGR, a plant will rapidly increase in size and is able to occupy a large space, both below and above ground. This appears consistent with plant strategy theory (Grime, 1979), which predicts that a plant with high relative growth rate has the opportunity to acquire a large share of limiting resources like nutrient or water than a slow growing species. A high RGR may also facilitate rapid completion of life cycle of a plant.

The result of present investigation suggested that RGR of grass *Echinochloa crus-galli* increased in response to competition. The increase in RGR suggested a facilitation rather than competition. Facilitation often offset the effect of competition (Peltzer and Kochy, 2001). Both facilitation and competition may operate simultaneously, resulting significant changes in overall growth (Callaway, 1995; Goldberg and Novoplansky, 1997). A slight increase in height may result in disproportionately large differences in light capture and thus NAR between neighboring plants (Ballard *et al.*, 1988, Ballare, 1994; Akram, 1998). The relative high NAR of grass *Echinochloa crus-galli* as compared to the weed species (Table-2), In present investigation the growth rate of grass *Echinochloa crus-galli* increase in competition^{+ve} and changes in RGR is determined by often changes in NAR. Furthermore a close link between RGR and NAR has reported by several workers (Eagles 1967; Pons 1977; Khan, 1973 and 1975; Ahamad and Rao, 1982). Garnier (1992) has compared the RGR of co-generic annual and perennial grasses and found that growth differences in NAR. However, these interpretations contradict the finding of Brewster and Barnes (1981) and Poorter and Remakes (1990). The climbing life forms generally maximize light interception, maximize shading of the neighbour and minimize self-shading. All these attributes increase photosynthesis and thus growth and provide a competitive advantage to a plant (Givnish, 1986).

CONCLUSIONS

In the present investigation, the grass *Echinochloa crus-galli* plants growing in competition^{+ve} shows high LAR than that of plants in competition^{-ve} (Table-2). LAR is determined by both LAR and SLA (Causton and Venus, 1981). This increase in LAR is largely determined by due to changes in LWR and often due to the changes in SLA. These results confirm the findings of Elias and Chadwick (1979); Poorter and Remakes (1990) and Garnier (1991, 1992). Across all species the tight positive relationship between RGR and LAR was driven almost entirely by SLA rater than by the proportion of mass allocated by the leaves. This central role of SLA in determining seedling potential RGR is thus general across European grasses, herbs and woody perennials (Poorter and Remkes, 1990; Garnier, 1992; Cornelissen *et al*., 1996).

This refers to the fact that amount of leaf area per unit total plant weight is more important (as related to light attenuation) than allocation of biomass per unit leaf area. The increased LAR enhances the RGR (Pearcy and Sims, 1994) and thus the competitive potential (Peltzer and Kochy, 2001). Thus the high RGR of grass *Echinochloa crus-galli* in competition^{+ve} can be attributed to NAR and LAR (Causton and Venus, 1981, Dasti, 1994). The decreased SLA suggested that in responses to competition certain anatomical modifications in leaves have occurred which decreased the physiological activity per unit leaf area. Mechanisms to increase competitive ability include adjustment of leaf biomass toward thinner and larger leaves (Pearcy and Sims, 1994) to be fully established, but it of importance that the higher RGR can be achieved through high SLA. Apparently rapidly growing plants produce leaves with a low investment in biomass to leaves (Dijkstra, 1989).

Differences in biomass allocation have been found in numbers of studies (Van Dobben, 1967; Jackson and Roy, 1986). The changes in net assimilation rate leads to changes in biomass allocation to stems and leaves. This agrees with the findings of Jackson and Cladwell (1989) that the plants shift by competition. Often reduced light availability due to shading of neighbors' plant (Photmorhogenic response) (Peltzer and Kochy, 2001) leads to an increase in allocation to shoots. Light availability decreased linearly with increasing neighbors shoot mass (Peltzer and Kochy, 2001).

REFERENCES

Ahmad S. and Rao M.R. 1982. Performance of maize, soyabean intercrop combination in the tropics, results of multi location study. Field crops. 5: 147-161.

Akram S. 1998. Cause and consequences of variation in some members of family cucurbitaceae. M. Sc. Thesis, B. Z. University, Multan, Pakistan.

Arredondo J. T., Jones T. A. and Johnson D. A. 1998. Seedling growth of inter-mountain perennial and weedy annual grasses. Journal of Range Management. 51: 584-589.

Baker H G. 1974. The evolution of weeds. Annual Review of Ecology and Systematics. 5: 1-24.

Ballare C.L. 1994. Light gaps. Sensing the light opportunities in highly dynamic canopy environments. M.M. Cladwell R.W Pearcy (Eds). Explanation of environmental heterogeneity by plants academic press, San Diego, C. A. pp.73-110.

Ballared C.L., Snachez R.A., Scopel A. L. and Ghesra C.M. 1988. Morphological responses of *Datura ferox* L. Seedlings to the presence of neighbors. Their relationship with canopy microclimate. Oecologia. 76: 288-293.

Baskin J. M., Nan X.Y. and Baskin C.C. 1999. A comparative study of the seedling- juvenile and flowering stages of the life cycle in an annual and a perennial species of Senna (Leguminosae: Caesalpinioideae). American Midland Naturalist. 141: 381-390.

Bellingham P.J., Duncan R.P., Lee W.G. and Buxton R.P. 2004. Seedling growth rate and survival do not predict invasiveness in naturalized woody plants in New Zealand. Oikos. 106: 308-316.

Blacquier T., Hotstra R. and Stolen. 1987. Ammonium and nitrate nutrition in *Plantago lanceolata* and *Plantago major* spp. 1 aspect of growth, chemicals composition and root respiration. Plant and Soil. 104: 129-141.

Brewster J.L., Barnes A. 1981. A comparison of relative growth of different individual plant and different cultivars of onion of diverse. Geographic origin at two temperature and two light intensities. Journal of Ecology. 18: 589-604.

Bryant J.P., Chausen T.P., Richard P.B., Mcarthy M.C., Warner R.A. 1987. Effect of nitrogen fertilization upon secondary chemistry and nutritive value of Quaken aspen (Populustremuloides michx) leaves for the ilarge aspen tortrix choristomnea contlictana walker. Oecologia. 73: 513-507.517.

Bunce J.A. 1986. Measurements and modelings of photosynthesis in field crops. CRC critical review in Plant Science. 4: 47-77.

Burns J.H. 2004. A comparison of invasive and non-invasive dayflowers (Commelinaceae) across experimental nutrient and water gradients. Diversity and Distributions. 10: 387-397.

Callaway R. 1995. Positive interaction among plants. Botanical review. 61: 306-349.

Causton D.R., Venus J.C. 1981. The biometry of plant growth. London, United Kingdom: Edward Arnold. p. 320.

Coley P.D. 1987. Interspecific variation in plant antiherbivore properties, the role of habitat quality and rate of disturbance. New Physiologist. 16: 251-263.

Cornelissen J.H., Castro- Diez P., Hunt R. 1996. Seedlings growth allocation and leaf attributes in a wide range of woody plant species and types Journal of Ecology. 84: 755-765.

Cronk Q.B.C., Fuller J.L. 1995. Plant invaders. New York, NY: Chapman and Hall. p. 255.

Daehler C.C. 2003. Performance comparisons of co-occurring native and alien invasive plants: implications for conservation and restoration. Annual Review of Ecology and Systematics. 34: 183-211.

Dasti A.A. 1994. Physiological responses to water stress in some subtropical arid zone grasses Ph.D. Thesis University of Wales Aberystwyth.

Dijkstra P., Lambers H. 1989. A physiological analysis of genetic variation in relative growth rate with in Plantago major L. Functional .Ecology. 3: 577-587.

Duncan D.B. 1955. Multiple range and multiple F test. Biometrics. 11: 1-42.
Eagles C.F. 1967. The effect of temperature on vegetative growth in climatic races of Datylic glomerata in controlled environment. Annals of Botany. 31: 31-39.

Elias C.O., Chadwick M.J. 1979. Growth characteristics of grass and legume cultivars and their potential for land reclamation. Journal of Applied Ecology. 16: 537-544.

Evans G.C. 1972. The quantitative analysis of plant growth. Berkeley: University of California Press. p. 761.

Firbank L.G., Cousens R., Mortimer A.M., Smith R.G.R. 1990. Effect of soil type on crop yield-weed density relationships between winter wheat and Bromus sterilis. Journal of Applied Ecology. 27: 308-318.

Garcia S.H., Escarre J Garnier E., Sans X.F. 2005. A comparative growth analysis between alien invader and native Senecio species with distinct distribution ranges. Ecoscience. 12: 35-43.

Garnier E. 1992. Growth analysis of co-generic annual and perennial grass species. Journal of Ecology. 80: 665-675.

Garnier E. 1991. Resource capture, biomass allocation and growth in herbaceous plants. Trends in Ecology and Evolution. 6: 126-131.

Givinish T.J. 1986. On the adaptive significance of leaf height in forest herbs. American Naturalist. 120: 353-381.

Godberg D.E., Novoplansky A. 1997. On the relative importance of competition in unproductive environments Journal of Ecology. 85: 409-418.

Gottlieb L.D. 1978. Allocation, growth rates and gas exchange in seedlings of Stephamatrica exigva spp. Coronria and its recent derivative S. Malhevrensis. American Journal of Botany. 65: 970-977.

Grime J.P. 1979. Plant strategies and vegetative process. Jhon Wiley, Chichester. UK.

Grime J.P., Hunt R. 1975. Relative growth-rate: its range and adaptive significance in a local flora. Journal of Ecology. 63: 393-422.

Grotkopp E., Rejmanek M., Rost T.L. 2002. Toward a causal explanation of plant invasiveness: seedling growth and life-history strategies of 29 pine (Pinus) species. American Naturalist. 159: 396-419.

Hamilton M.A., Murray B.R., Cadotte M.W., Hose G.C., Baker A.C., Harris C.J. Licari D. 2005. Life-history correlates of plant invasiveness at regional and continental scales. Ecology Letters. 8: 1066-1074.

Hoffmann W.A., Poorter H. 2002.Avoiding bias in calculations of relative growth rate. Annals of Botany. 80: 37-42.

Huante P., Rincon E. and Acosta I. 1995. Nutrient availability and growth rate of 34 woody species from a tropical deciduous forest in Maxico. Functional Ecology. 90: 849- 858.

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

Hunt R, Nicholls A.I. and Fathey S.A. 1987. Growth and root-shoot partitioning in eighteen Brithis grasses. Oikos. 50: 53-59.

Jackson R.B. and Cladwell M.M. 1989. The timing and degree of root proliferation in fertile soil micro-sites for three cold desert 583. perennials. Oecologia. 81: 149-153.

Jackson L. E. and Roy J. 1986. Growth pattern of Mediterranean annual and perennial grass unclear stimulated rainfall regimes of southern France and California. Oecologia. 81: 149-153.

Keddy P.A. 1992. A pragmatic approach to functional ecology. Functional Ecology. 6: 621-626.

Khan D.K.M. 1973. Growth and genetic analysis of rice of plant. M. Sc. Thesis. University of Agriculture Faisalabad, Pakistan.

Konings H. 1989. Physiological and morphological differences between plants with a high NAR or a high LAR as related to environmental conditions. In: H. Lambers (Ed.). Causes and consequences of variation in growth rate and productivity of higher plants. The Hague, Netherlands: SPB Academic Publishing. pp. 101-123.

Kropff M.J. and Spitters C.J.T. 1991. A simple model of crop loss by wheat competition from early observations on relative leaf area of the weeds. Weed Research. 31: 97-105.

Lake J.C., Leishman M.R. 2004. Invasion success of exotic plants in natural ecosystems: the role of disturbance, plant attributes and freedom from herbivores. Biological Conservation. 117: 215-226.

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

Lambers H., Freijsen I.V., Pooter H., Hirose T. and Vancler W.A. 1989. Analysis of growth base on net assimilation rate and nitrogen productivity. Their physiological background causes and consequence of variation in growth rate and productivity of higher plants. H. Lambers, ML. Cambridge, H. Konnings and TL. Pons (Ed.). SPB Academic Publishing the Magve. pp. 1017-1018.

Lambers H. and Dijkstra P. 1987. A physiological analysis in genotypic variation in relative growth rate: can growth rate confer ecological advantage? In: J. van Andel, J. P. Bakker, and R. W. Snaydon (Eds.). Disturbance in grasslands. Dordrecht, Netherlands: Junk Publisher, Dordrecht. pp. 237-252.

Nieman G.J., Pureveen J.B.M., Eijkel G.B., Pooter H. and Boon J.J. 1992. Difference in relative growth rate in grasses correlate with differences in chemical composition determine by pyrolysis moss spectrometry. Oecologia. 89: 567-573.

Oksanen L., Oksan T., Lukkari A. and Siren S. 1978. The role of phenol based inducible defense in the interaction between tundra populations of the role *Clethrionomys rufcanus* and the dwarf shrub *Vaccinium myrthillus*. Oikios. 50: 317-380.

Panday R.K., Saxener M.C. and Singh V.B. 1980. Growth analysis of Urd bean (*Vigna mungo* L.) genotypes under humid subtropical conditions of Plant ages (India). Legume Research. 1(2): 59-63.

Panthis J.D., Diamantolov S. and Margaris N.S. 1987. Altitudinal variation in total lipid and soluble sugar content in herbaceous plants on mount Olympus (Greece) Vegetation. 72: 21-25.

Pattison R.R., Goldstein G. and Ares A. 1998. Growth, biomass allocation and photosynthesis of invasive and native Hawaiian rainforest species. Oecologia. 117: 449-459.

Pearcy R.W. and Sims. 1994. Photosynthesis acclimation to changing light environment scaling from the leaves to the whole plant. pp. 145-174. In: MM. Mcland well and R.W. Pearcy (eds). Explanation of environmental heterogeneity by plants. Ecophgysiological processes above and below ground. Academic Press Son diego CA.

Peltzer Kochy D.A. 2001. Competitive effects of grasses and woody plants in mixed- grass praire. Journal of Ecology. 89: 519-527.

Pons T.L. 1977. An ecophysiological study in the field layer of ash coppice II experiments with *Geum verburnum* and *Cirsium palustre* in different light intensities. Acta Botanica neerandica. 26: 251-263.

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

Poorter H. 1989. Interspecific variation in relative growth rate: on ecological causes and physiological consequences. In: H. Lambers (Ed.). Causes and consequences of variation in growth rate and productivity of higher plants. The Hague, Netherlands: SPB Academic Publishing. pp. 45-68.

Richards J. and Caldwell M.M. 1985. Soluble carbohydrates, concurrent photosynthesis and efficiency on growth following defoliation: a field study with

Agropyron species. Journal of Applied Ecology. 22: 907-920.

Riech P.B., Walters M.B. and Ellsworth D.S. 1992. Leaf life span in relation to leaf, plant and stand characteristics among diverse ecosystems. Ecological monograph. 62: 365-392.

Shipley B. 2006. Net assimilation rate, specific leaf area and leaf mass ratio: which is most closely correlated with relative growth rate? A meta-analysis. Functional Ecology. 20: 565-574.

Vandobben W.H. 1967. Physiology of growth in two Senecio species in relation to their ecological position. Madeleine Van Institute Voor biogischen scheikanfig onderzoex van land Bouwge Wesson. 346: 75-83.

Ven de werst A., Van nevnen M., Visser A.J. and Lambers H. 1993. Contribution of physiological and morphological plant traits to species competitive ability at high and low nutrient supply. Oecologies. 94: 434-440.

Villar R., Arenas F., Lambers H., Panadero P., Maranon T. and Quero J.L. 2005. Variation in relative growth rate of 20 Aegilops species (Poaceae) in the field: the importance of net assimilation rate or specific leaf area depends on the time scale. Plant and Soil. 272: 11-27.

Wardle D.A. and Nicholson K.S. 1996. Synergistic effects of grass land plant species on soil microbial biomass and activity: implication for ecosystems level effects of enriched plant diversity. Functional Ecology. 10: 410-416.

Weaver S.E. 1996. Simulation of crop- weed competition: models and their applications. Phytoprotection. 77: 3-11.

Wilson S.D. and Tilman D. 1995. Competition responses of eight old- field plant species in our environments. Ecology. 76: 1169-1180.