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Biomass in Evolving World - Individual's Point of View

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1. Introduction

For a long time, ecology has been criticized for being primarily descriptive science concentrated on the 'What' question rather than progressing further into the 'Why' and 'How' domains (O'Connor, 2000). Over the past few decades, however, ecology has moved toward dynamic mechanistic and more strongly predictive science (Kearney et al., 2010). It is becoming increasingly clear that to comprehend mechanisms underlying population dynamics, demography and ecological breadth it is necessary to regard the fact that discrete organisms, which constitute populations, might have different individual responses to ontogenetic and environmental cues (Begon et al., 1990). The challenge is, as noted by Kearney et al. (2010), "to derive an approach for studying penetrance of functional traits of individual organisms into higher, group-level phenomena".

Generally, the interdependency of population-level and individual-level processes is very complex. Although population is composed of individuals, it has emergent properties that are more than just the sum of the properties of individuals. Organisms come to life and die on particular days, but populations have birth and death rates. At any specific moment, individuals are of certain age, but populations have age structure which is very important for determining population growth. Individual characteristics, such as size, growth pattern, age at maturity, number of offspring and longevity, greatly influence population dynamics, but, on the other hand, physiology and patterns of growth and development of each organism depend both on its genotype and on population properties such as the number, sizes and spatial distribution of other individuals. Therefore, the relationship between organisms and their populations is reflexive; phenomena at one biological level are both the cause and the consequence of the phenomena on other.

This chapter is dealing with individual level processes – biomass allocation strategy, allometric growth and phenotypic plasticity. How these developmental processes may affect population dynamics will also be discussed.

2. Individual-level phenomena

2.1 Allometry and allocation strategy

Allometry (Greek *allos*, "other", and *metron*, "measure"; Huxley, 1932) is the study of size-correlated variations in biological forms and processes. Niklas (1994) recognizes three conceptual and methodological meanings of this term: 1) the growth of one part of an

organism in relation to the growth of the whole organism or some other part of it, 2) the study of the consequences of size on organic form or process, and 3) any departure from geometry and shape that is conserved among a series of objects differing in size. Literally, allometry means unequal growth of organs during development of an organism. The fundamental biological principle presumes that acquisition of external resources and metabolism, producing energy and materials for all biological processes, enable organisms to grow in size (i.e., enlarge biomass). However, in biological systems, increase in absolute size always goes along with modifications in relative sizes of organismal parts. In other words, by growing larger, individuals alter their shape; growth itself is size-dependent, i.e. allometric (Weiner, 2004). This process is a consequence of inherent continuous changes in directions of biomass allocation into different structures and activities during the course of development, and reflects alterations in priorities at any point of time of individual ontogenesis. For example, early in development, after germination and emergence of radicle (part of a plant embryo which develops in a root), plants have more roots than shoots. Later, as they grow, relative allocation into aboveground structures increases and results in more 'shooty' individuals. A late fetus has a larger head and shorter legs in relation to its body length than an adult human. Alteration in growth pattern during human ontogeny accounts for later changes in body part proportions. Metabolic rates and the heat produced by metabolism increase less rapidly than total body size.

From the ecological point of view, biomass allocation strategy plays a critical role in determining organismal ability to survive and reproduce (i.e., fitness). If an ideal organism would exist, it would be mature at birth, continuously produce a large number of high-quality offspring, and live forever. Such an organism, called 'Darwinian demon' (Law, 1979), would bedevil all other organisms. The same creature, named 'Hutchinsonian demon' in community ecology, would dominate in its habitat because it would be the best in colonizing new patches, utilizing all the resources, avoiding predators and resisting stresses (Kneitel & Chase, 2004), and, eventually, it would monopolize the life on Earth. In reality, however, the existence of such an organism is impossible because: 1) the amount of resources (i.e., nutrients and energy) that an organism can acquire is finite, and 2) a proportion of the resources allocated to one activity (for example to growth, that is to somatic maintenance and survival), decreases the amount of resources that can be allocated to another (e.g., to reproduction). As noted by Stearns (1992), "allocation decisions between two or more processes that compete directly with one another for limited resources within a single individual" imply mutually exclusive allocation, or **physiological trade-off**.

If an increase in fitness due to a change in one trait is opposed by a decrease in fitness due to a concomitant change in the second trait, it is clear that adaptive growth strategy in one environment depends on optimal balance of biomass allocation between different organismal functions (Roff & Fairbairn, 2007). Individuals must allocate resources in a way that make the most of their chances for contributing offspring to the next generation while simultaneously maximizing their chance of surviving to reproduce (Gurevitch et al., 2002). Among characteristics that figure directly in reproduction and survival, and are often in trade-off between each other, Stearns (1992) indicated several principal life-history traits: size at birth, growth pattern, age at maturity, size at maturity, number, size and sex ratio of offspring, age- and size-specific reproductive investments, age- and size-specific mortality schedules, and length of life. Correlations between these traits may be positive or negative (trade-offs), but eventually they combine in many different ways to produce diverse schedules and durations of key events in an organism's lifetime. Logically, natural selection

in one environment may prioritize some capabilities at the expense of others. As a consequence, different life-histories evolve.

2.2.1 The evolution of life-histories

The developmental paths that describe changes in form ("ontogenetic trajectory"; Magwene, 2001) and life-history schedule are often considered to be genetically determined, i.e., species- or genotype-specific (Weiner, 2004), and/or the products of biomechanical and other physical constraints (Givnish, 1986). These assertions have been brought into question by the well documented fact that allometry itself can be plastic and trade-offs may vary with environmental variations (e.g., Cheplick, 1995; Weiner, 2004), as well as because a significant degree of variability in life-histories can exist within populations. However, they still can serve as a starting point for understanding life-history evolution. Comparative biology has demonstrated a great variety of life-histories at the level of species and higher taxonomic groups. In plants, besides tremendous variation in life-cycle patterns, from annual semelparous forms to long-lived iteroparous woody perennials, interesting variations can be found in growth architecture of clonal plants with vegetative reproduction. Lovett Doust (1981) made characterization of these clonal forms on a continuum between 'phalanx', in which vegetative clones (ramets) of one parental plant are grouped tightly together, and 'guerilla' form, which is presented with ramets dispersed like guerilla forces. Vegetative reproduction makes an interesting case on the diversity of life-histories. For example, in quaking aspen (*Populus tremuloides*) individual trunks, which are genetically identical to their paternal plant, live for about 50 years, while the genotype composed of many individual plants, may live for more than 10 000 years. In animals, some species mature early and reproduce quickly, have small body size and a large number of eggs (e.g., many insects), whereas in other species maturation is delayed for several years, individuals are large and have a small number of offspring (e.g., some mammals). Between these extremes, a great variety of different combinations of life-history schedules and growth forms exists.

Although it is reasonable to presume that there is individual variability within each species, relations between life-history traits differ substantially more between higher taxonomic groups. Darwin elegantly explained this phenomenon – related species descended from a common ancestor and shared common evolutionary history for a long time. These 'lineage-specific effects' emphasize characteristics that are general for a group of related species or higher taxonomic levels. The comparative analyses of species, genera, families and classes demonstrate broad patterns of the evolution of allometry, trade-offs and life-history. The examples of how lineage-specific mode of growth affects metabolic and growth rates, and reproduction, can be found all over the living world. Major groups of ectothermal and endothermal organisms have different metabolisms and different growth rates per unit weight during growth, which is involved in determination of age at maturity and the cost of reproduction. For ectothermal organisms, about thirty times less energy supply is needed for the same growth rate as for endothermal (Peters, 1983). Organisms with determinate growth (e.g., annual plants, birds, mammals, and most insects) stop growing when mature, whereas allocation of energy between growth and reproduction continues through adult life for organisms with indeterminate growth, such as perennial plants, fish, amphibians, reptiles, etc. That means that 'allocation decision' between growth and reproduction is made only once for the first group, and many times for the second (Stearns, 1992). The analyses of more than 500 mammal species (Wootton, 1987) imply that body mass is positively correlated with age at first reproduction. Age at maturity is also positively correlated with

adult lifespan within lineages of birds, mammals, some reptiles and fishes, although the relationships between the two life-history traits differ among these large groups. If corrected for body size, the data suggests that increase in longevity with delay of reproduction is the highest for birds and mammals (Charnov & Berrigan, 1990).

The results of comparative analyses of higher taxonomic groups imply that changes in life-histories are phylogenetically constrained in some degree, as a result of shared evolutionary history, genes and developmental pathways. However, it must be kept in mind that comparative biology provides information about boundary conditions on life-history evolution, but, within each lineage, populations and species differ and follow their own patterns of life-history adaptation to specific environment. Here, natural selection acts on life-histories to adjust biomass allocation in a way that maximizes total lifetime fitness. The genotypes (organisms) that have the ability to distribute their resources optimally for certain ecological conditions, will reach the highest fitness and their frequencies in next generations will rise. Those patterns of biomass allocation that present responses of populations to natural selection, Stearns (1992) defines as **microevolutionary trade-offs**. The relationship between individual-level (i.e., physiological trade-offs) and population-level (i.e., microevolutionary trade-offs) is inevitably complex. The physical division of limited materials and energy supply within an organism is a boundary condition on the evolutionary optimization of life-history strategy within a population inhabiting certain environment. However, the ability of organisms to optimally distribute their biomass and/or to alter the pattern of allocation in accordance with environmental change depends on evolutionary changes of genetic variation in a population. In other words, microevolutionary trade-offs set a trade-off structure that is a constraint for physiological trade-offs.

Intra-individual trade-offs depend on the amount of available resources and interactions between organisms, or in other words, they are plastic. To understand the nature of complex and dynamic relations between different types of trade-offs, which impose both constraints and a basis for their evolution, environmental influences on allometric patterns must be analyzed.

2.2.1.1 Plastic allometry

It is a common knowledge that the fitness of an individual depends both on its genotype and its environment. When live in variable abiotic and biotic circumstances, organisms may achieve high fitness by changing their growth and life-histories so as to match the most fit trait values for each set of environmental conditions. This property of a genotype to express different phenotypes in distinct environments is called **phenotypic plasticity**, and the way that trait expression varies across a range of environments for a given genotype is called its **norm of reaction** (Bradshaw, 1965; West-Eberhard, 1989). From the allometric point of view, plasticity can be understood as a change in allometric growth/allocation patterns in response to the environment (Schmid & Weiner, 1993). According to the optimal allocation theory, organisms should allocate more resources to organs that capture the most limiting resource and less to organs that are involved in obtaining non-limiting resources. At the same time, as was previously noted, they must optimize biomass allocation into reproductive function in order to produce the highest possible number of quality offspring while limiting the losses for their own survival. The solution of this incredibly complex task depends on the characteristics of a population and physical environment. Besides variability in genetic background of their life-history strategies, individuals within a population may

also differ significantly in their ability to cope with external conditions. Different genotypes may respond differently to the same environment, and this variability in reaction norm for allocation patterns accounts for the total phenotypic variation. As noted by Stearns (1992), microevolutionary trade-offs may evolve, or, in other words, population can respond to selection, if there is genetic variation for this reaction norm (i.e., for physiological trade-offs).

Before we explore some examples of relations between life-histories and their plasticity, several properties of phenotypic plasticity have to be explained. As a measure of change in genotype's trait value between different environments, plasticity need not always be adaptive. Some alterations in individual appearance and function are merely unavoidable consequences of organismal physiology (Sultan, 1995). Disadvantageous (maladaptive) plasticity may results from organismal inability to maintain a constant phenotype when faced with environmental circumstances despite fitness reduction due to variation (Alpert & Simms, 2002). For example, in low-quality environments, or under intense competition for resources, organisms are smaller compared with those in rich-environments; plants have yellow leaves when deprived of sufficient nitrogen, or have lower photosynthetic rate under low light intensity. In ecology, it is common to measure plasticity of a species as a range of ecological conditions that a species can grow in; this measure is also called species' niche (Grinell, 1917). Also, it is common to assign a species as generalist or specialist. However, it must be kept in mind that the niche of each species is determined by the sum of niches (i.e., reaction norms) of its members that may be plastic or nonplastic (Gurevitch, 2002). This is a very important remark for understanding life-history evolution – we can define life-history for each species, but its plastic responses to environmental changes give the opportunity for further evolution of life-histories.

Plasticity of trade-offs between life history traits have been demonstrated in a large number of studies and numerous taxa in laboratory and natural populations (e.g., Reznick, 1985; Sinervo & DeNardo, 1996; Zuk, 1996; Tucić et al. 1997, 1998; Tucić & Stojković 2001; Roff, 2002; Stojković et al. 2009). The number of possible relations between different life-history traits is great, and the ways in which they can change under various environmental conditions is, logically, much greater. Here, I present just a few examples to illustrate both the theoretical and empirical knowledge on life-history/allometry plasticity.

The allometry plasticity can be demonstrated with one of the best understood adaptive plastic systems in plants, generally termed as the 'shade avoidance' syndrome (Smith & Whitelam, 1997). Plants are able to detect low ratio of red to far-red radiation (R:FR) in ambient light as the first signal of future competitive interactions, well before mutual shading actually occurs (Ballaré et al., 1987, 1990). Because chlorophyll preferentially absorbs red light, radiation transmitted through or reflected from a leaf canopy exhibits lower R:FR ratio than does full sunlight (Smith et al., 1990). Therefore, the R:FR ratio can be seen as an environmental, external, cue of population density. It triggers a suite of photomorphogenic plastic responses (e.g., stem elongation, branching reduction, acceleration of flowering) that enables plants to minimize effects of mutual shading by neighbours and maximize the ability to deny light to proximal plants (Aarsen, 1995). The allometric shift in plant growth form is achieved through an increased shoot extension rate coupled with a strong apical dominance (main stem dominance). In crowded conditions this growth pattern enables plants to acquire more radiant energy for photosynthesis and improve their final performance. In uncrowded situations, however, elongation of stems has more costs than benefits. More resources must be allocated into support structures rather than to flowers and seeds. That is why elongated growth form of plants is adaptive only in

dense environment. Many experiments on plants strongly corroborated the evolutionary ecological prediction that the shade avoidance phenotype is indeed an adaptation, likely moulded by natural selection from competition for light (Dudley & Schmitt, 1996; Schmitt, 1997; Schwinning & Weiner, 1998; Tucić & Stojković, 2001).

In the study on perennial clonal species *Lamium maculatum*, Stojković et al. (2009) have shown that genotype by environment interaction could change the proportion of biomass allocated into reproductive function. The goal of the experiment was to analyze changes in biomass allocation patterns across genetically structured populations where plants are competing for access to light. Clonal replicates of 17 genotypes were grown under three regimes: 1) control (C; low level of competition), 2) intraclonal competition (S; competition between clones of the same genotype) and, 3) interclonal competition (M; competition between plants of different genotypes). It was shown that the growth of these plants was sensitive to genetic identity of competitors, and that the competition between genetically

Allometric relationship	Treatment	R^2	*P*	α	Test of isometry (Ho: α = 1) F	*P*
logFW: log(SW+LW+RW)	C	0.00	0.720	2.52^{A}	105.36	0.000
	S	0.10	0.003	1.99^{A}	52.39	0.000
	M	0.24	0.000	1.59^{B}	22.77	0.000
logSW: log(FW+LW+RW)	C	0.80	0.000	1.18^{A}	14.02	0.000
	S	0.89	0.000	1.07^{A}	3.37	0.070
	M	0.89	0.000	0.99^{B}	0.04	0.841
logLW: log(FW+SW+RW)	C	0.64	0.000	$0.82_{A(e)}$	10.92	0.001
	S	0.79	0.000	$0.80_{B(e)}$	22.37	0.000
	M	0.83	0.000	$0.78_{C(e)}$	33.75	0.000
logRW: log(FW+SW+LW)	C	0.68	0.000	$1.41_{B(e)}$	37.39	0.000
	S	0.75	0.000	$1.54_{A(e)}$	73.31	0.000
	M	0.86	0.000	$1.53_{A(e)}$	119.84	0.000

Table 1. Standardized major axis tests of the allometric relationship (log scaled variables) for reproductive effort (FW) and relative biomass investments to stems (SW), leaves (LW) and roots (RW) based on weight measures of *L. maculatum* plants grown in three experimental treatments (control - C, intraclonal - S and interclonal - M competition). Scaling slope α, R^2 and *P* values for correlations within treatments are reported. Results of pairwise slope comparisons between treatments (based on 1000 iteration in permutation testing) are presented as letters in superscript. If differences among slopes were insignificant, pairwise tests of shift in elevation were performed and results presented as letters in subscript [(e)-elevation]. Identical letters indicate insignificant difference of either slopes or elevation between treatments. Letter A points to the largest value. F statistics and *P* values of the test of differences between observed slope within treatments and α=1 are reported as statistics of isometry testing (Stojković et al., 2009).

unrelated individuals was the most stressful environment for this plant species (the indices of competition intensity were the highest in this treatment, unpublished data). Analyses of allometric growth (mathematical procedure of this analysis will be explained later) revealed that in resource-rich, noncompetitive environment, where absolute fecundity is the highest, allocation to reproduction (flower weight - FW) is less determined by the size of plants than in competitive condition (insignificant correlation between flower weight and vegetative weight, $P = 0.720$, Table 1).

On the other hand, allocation patterns into reproductive function differed considerably between S and M treatments (Table 1). First, it was shown that relationship between weights of vegetative and reproduction modules was anisometric (slope of allometric relation significantly larger than 1), indicating that relative biomass allocation to reproductive effort was greater for larger plants in competition, which achieved higher reproductive outcome. As was shown in the analyses of two treatments with different genetic identity of competitors, small individuals in intense competition (interclonal) tended to allocate larger proportion of acquired resources to reproductive organs compared with small plants in less intense competition (intraclonal). The reverse is true for larger plants suggesting that successful, big individuals in severe asymmetric interaction can balance more productively between vegetative and reproductive fitness components than smaller plants. This conclusion was based on a significantly slighter allometric slope in interclonal competition ($\alpha = 1.59$, $P < 0.000$ for M; $\alpha = 1.99$, $P < 0.003$ for S; Table 1, Figure 1).

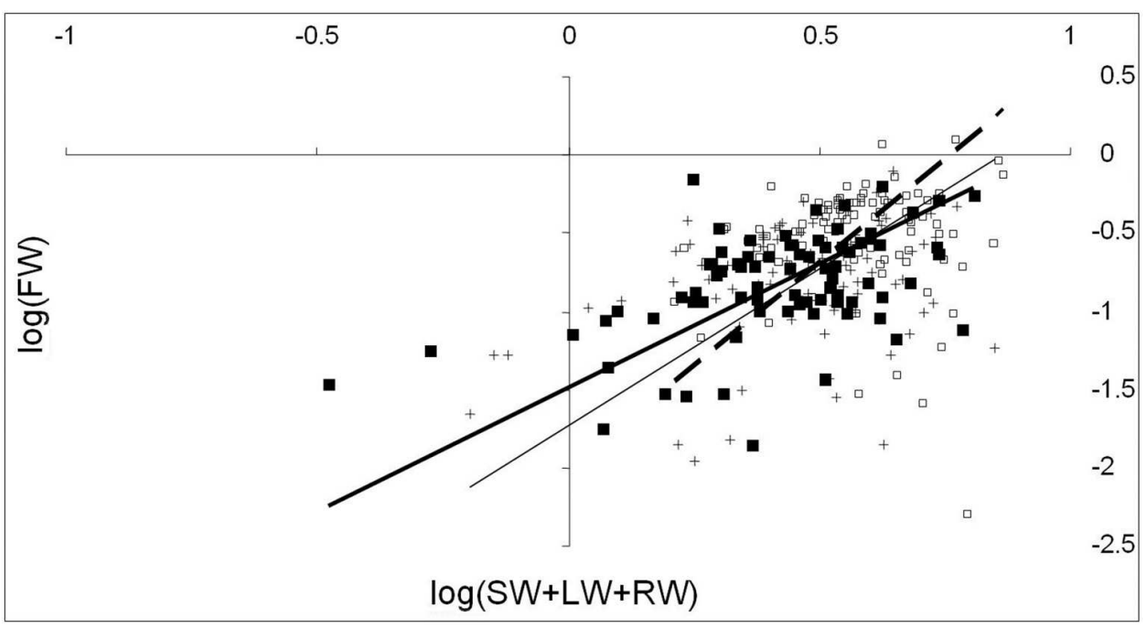

Fig. 1. The allometric relationship (log scaled variables) between reproductive effort (flower weight; FW) and allocation to vegetative modules for *L. maculatum* grown in three experimental treatments (control, intraclonal and interclonal competition). The SMA allometric function plotted through the individuals in control treatment (dashed line), intraclonal competition (thin line) and interclonal competition (thick line). Symbols for individuals in control (□), intraclonal (+) and interclonal (■) competition (Stojković et al., 2009).

Allocation analyses between other plant organs (weight of flowers, stems, leaves and roots) also suggested that in *L. maculatum* specific allometry strategy of smaller plants in intense competition with unrelated individuals could reflect trade-offs in favor of reproductive effort, both directly via allocation to flowers and indirectly into stems (i.e., to new plant meristems which could be committed to reproductive function). Such investment to flowers may be beneficial for smaller individuals because allocation of limited acquired biomass to extensive vegetative growth (e.g., leaves) may leave insufficient time for successful reproduction before the end of growing season (Bonser & Aarssen, 2001). Many studies reported that plants grown in competitive environments invested relatively more in sexual reproduction (e.g., Prati & Schmid 2000; Van Kleunen et al., 2002).

Phenotypic plasticity of correlations between life-history traits has been confirmed in many insect species. In order to analyze trade-off between the size and number of eggs, Fox et al. (1997) performed a study on seed beetle *Stator limbatus*. These beetles develop completely inside seeds of over 50 different host plants, and emerge from seeds as adults. In their experiments, Fox and colleagues reared beetles on acacia (*Acacia greggii*) which is a good host, and a palo verde (*Cercidium floridum*) suboptimal host on which survival of larvae is less than 50%. Several presumptions from life-history theory were made: 1) there is a trade-off between size and number of offspring, i.e., the same amount of resources can be allocated into large number of small offspring, or into few big ones, 2) a probability of survival for any individual offspring is an increasing function of its size, and 3) the minimum size for offspring survival is smaller on the good host. If these assumptions are correct, females of *S. limbatus* should lay larger eggs on the poor host than on the good host. The study confirmed this hypothesis – females adjusted the size of eggs to the host on which they laid, and, also, these larger eggs came at cost of fewer egg produced over a lifetime. Additionally, it was shown that the production of larger eggs was adaptive. Survival of larvae hatching from small eggs was less than 1%, whereas 24% of the larvae hatching from large eggs survived to adulthood on suboptimal host. On the other hand, since the majority of larvae that developed on acacia seeds survive, higher lifetime reproductive success of females is achieved by producing more and smaller eggs. Berrigan (1991) performed meta-analysis of the relationship between egg size and number in three orders of insects and found negative correlations (i.e., trade-off) among these life-history traits.

One of the most important determinants of life-history evolution is 'age-specific selection' (Rose, 1991; Charlesworth, 1994) which is well described through several major trade-offs: between time schedules of reproduction and longevity, early and late fecundity, reproduction and growth, etc. Evolutionary changes in allocation strategy between different life-history traits have been continuously detected in laboratory evolution experiments on *Acanthoscelides obtectus* (Tucić et al., 1997, 1998). The methodology of experimental evolution is a valuable research tool for the study of basic mechanisms that shape individual life-history because it provides opportunity for testing direct and correlated responses to selection. In the laboratory of these researchers, seed beetle *A. obtectus* has been selected to reproduce either early (E selection line) or late in life (L selection line). About 200 generations of selection for early reproduction gave rise to beetles with enhanced fitness during early life, a short life span and small body size. On the other hand, adults of both sexes selected for late-reproduction are bigger, live longer, and have increased late fecundity and total fecundity compared with beetles from the E treatment. During the course of age-specific selection on *A. obtectus*, at least two trade-offs were experimentally documented: the

trade-off between late fecundity and early fecundity and among early fecundity and longevity (Tucić et al., 1997).

Clearly, the complexity and dynamic relations between life-histories of organisms and their environments suggest that allometric patterns evolve in response to numerous selection pressures and constraints. But, how these processes can influence the 'behaviour' of populations? These problems will be discussed after a short description of mathematical procedures that are currently used in the analyses of allometry.

3. Allometry analysis

For the adequate empirical and analytical treatment of allometric phenomena in ecological studies it is important to estimate the relationship between two variables, or, in other words, to determine how one variable scales against another. Variables represent different measures of individuals in a sample, such as weight and length of some organismal parts (organs or modules), multivariate shape or size, number of specific modules (for example, leaves, stems, flowers, roots in plants), life-history traits (e.g. life span, fecundity, growth rate, age at first reproduction), metabolic rate (e.g. activity of enzymes, hormones), etc. The main goal of this approach is to understand the allocation patterns within certain species, populations and/or environments.

The general 'allometric equation' that describes relationship between two variables is

$$y = \gamma \cdot x^{\alpha}$$

where y and x are biological variables, γ is the 'scaling (proportionality) coefficient' and a is 'scaling exponent'. a and γ parameters describe the functional (mathematical) relation between x and y.

It can be converted into linear relationship between x and y if variables are log-transformed, so the above formula can be reexpressed as

$$\log(y) = \log(\gamma) + \alpha \log(x)$$

or

$$Y = \beta + \alpha X$$

where substitutions are made: Y=log(y), X=log(x) and β=log(γ). Now, β is the value of Y where it intercepts the vertical axis, and a is equal to the slope of linear function when plotted on logarithmic scale. The log transformation is useful for several reasons: 1) it allows the relationship between the two variables to be expressed as a linear relationship, 2) it puts the variables on a multiplicative or logarithmic scale, which tend to diminish differences among large numbers and accentuate differences among small numbers, 3) it may transform frequency distribution of the data into normal distribution, and 4) it reduces statistical problems resulting from a number of outlying data points.

There are several statistical procedures for finding the line of best fitting through a bivariate cloud of data – linear regression, major axis, standardized major axis and their modifications. Several authors (e.g. Niklas, 1994; Bonser & Aarssen, 2001, 2003; Warton et al., 2006) proposed standardized major axis (SMA) method (or reduced major axis, RMA) on log-transformed variables as the most appropriate for allometry analyses. Falster et al.

(2003) developed statistical software, (S)MATR, for application of SMA method in studies of allometry patterns.

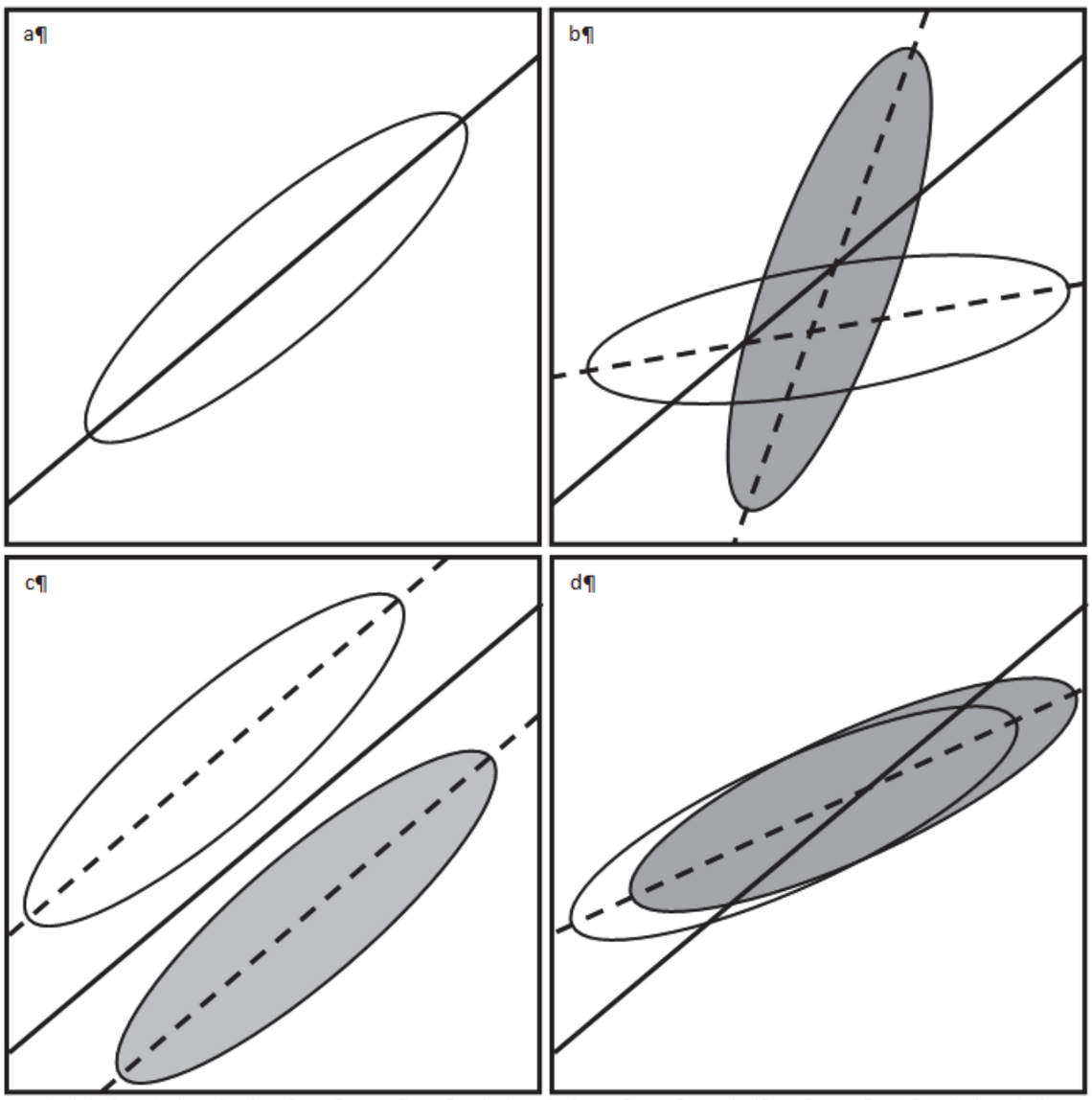

Fig. 2. Illustration of different types of allometric analyses in (S)MATR statistical software (Falster et al., 2003): (a) test of the isometry (α = 1); (b) testing if slopes of allometric function are different between groups; (c) testing if elevations are different between groups; (d) testing for shift along the axis. (After Falster et al., 2003)

SMA methodology is appropriate where there is error in both the x and y variables of the regression models and when we are not interested in prediction but to estimate the line-of-best-fit relating two variables, which is the basic purpose of allometry estimates (Warton et al., 2006). A significant allometric relationship is indicated where the slope (α) of the relationship between logarithms of the two variables differs from isometry. An isometric relationship between biological variables (α = 1) implies that the relative biomass allocation

to one organ or function is proportional to the allocation to other organ or function (Figure 2a). The best way to understand isometry and allometry is to imagine that one of the variables in the allocation analysis is some measure of the size of the whole organisms (for example, total weight or height). Then, isometry suggests that relative biomass allocation to specific organ or function is constant for all individual sizes. For example, the size of adult human heads would be several times greater than it is, if the growth of human fetus would proceed in isometric fashion. If the relative allocation to some organ or biological function is greater for larger individuals, than the scaling exponent, or slope of allometric relationships between the two variables is greater than one ($\alpha > 1$; Figure 2b). On the other hand, lower relative investment into one organ during the growth of an organism is detected as a value of scaling exponent that is less than one ($\alpha < 1$; Figure 2b). In the experiment on *Lamium maculatum* (Stojković et al., 2001), the biomass allocation into reproductive organs (flowers) and roots was generally greater for larger individuals, indicating that high ability of biomass acquisition was correlated with development of roots and, also, that these plants invested disproportionately high amount of energy and materials were into future offspring (Table 1, Figure 1). On the other hand, allocation of biomass into stems was shown to be isometric, i.e., directly proportional to the weight of other plant organs, whereas investment into leaves was greater for small plants (Table 1). These patterns of allocation suggested that when plants compete for the access to light, there was a difference in allometry strategy between different size classes of individuals – small plants invested more resources to organs that capture the most limiting resource (light) than larger plants. Allometry analysis gives the opportunity to answer some more questions about the nature of growth and differences between groups of organisms. For example, although the relative proportions of biomass allocated into one organ or biological function may be similar between groups (have a common allometric slope), two groups can differ in absolute values of biomass measures. Then, two groups can differ in elevation (i.e., intercepts) of their allometric function (Figure 2c), or they can diverge along a common axis (Figure 2d). In the study on *L. maculatum*, for plants with similar sum weights of flowers, roots and stems, the weights of leaves were significantly lower in competition, especially in the treatment with the most intense competition. This result indicated that plants in different competition treatment had different opportunities for acquiring resources. Although, as was noted above, an adaptive strategy of plants in competition for light (especially for small individuals) may be allocation into leaves, the difference in average absolute weights (C > S > M) resulted in observed shift in elevation (Table 1).

Negative value of slope of allometric relationship is particularly important for life-history studies because it indicates the trade-off between different functions of organisms, for example between developmental rate and life span, or between fertility and longevity.

4. Individuals versus populations

Many ecological processes in populations and communities may be understood in terms of size and/or life-history allometric patterns. In other words, the way the individual growth and life-histories are shaped in certain environment could largely influence the demographic patterns of a population. For example, changes in life-history schedules of members of a population can change population demography parameters, such as rate of population growth and carrying capacity. The trade-off between seed size and seed number has been used as an explanation for difference in competition and colonization abilities of

plant species. As suggested, competitive ability is enhanced by production of fewer, larger seeds, whereas colonization ability is improved by production of many small seeds (Turnbull et al., 1999; Levine & Rees, 2002). The members of natural populations often differ in size and relatedness to each other, which may affect the division of limited resources and have consequences on reproductive success, changes in the ratio of birth rate/mortality rate, and influence population growth in different ways (Aikio & Pakkasmaa, 2003).

Here, we explore several theoretical deductions about the relationship between individual and population level responses to competition intensity, i.e. density.

4.1 The 'rules' in plant ecology

"Plant growth is highly plastic, and the mass, height, number of leaves, and reproductive output of an individual plant can vary over orders of magnitude depending on growth conditions." (Gurevitch et al., 2002)

One of the regularities that were revealed in plant populations regarding competitive interaction was that the total final dry weight per unit area of all plants in a population is remarkably consistent over a wide range of densities. In other word, the average individual plant size became smaller as density increase, but this reduction is in linear relationship with increasing number of individuals per unit area (Kira et al., 1953). As a final result, total biomass will be the same for different population densities.

Regularity has been also found in the relationship between the size of a plant population (density), size of individual plant and mortality rate. For some time, this regularity has been considered as an ecological 'law' or 'first principle', and is known as '-3/2 self-thinning rule' (Yoda et al., 1963):

$$M=kN^{-3/2}$$

According to this rule, the average individual plant biomass (M) in a population is proportional to the -3/2 power of population density (N); *k* is a constant that differs among species. If N increases, M will decrease anisometrically as a consequence of density-dependent mortality, or 'self-thinning'. During the growth of seedlings, crowding becomes severe, and some individuals, usually the smallest and weakest ones, begin to die. The more plants are crowded the sooner and at smaller individual sizes mortality will begin. As a result, in less crowded plant populations, individuals may achieve larger sizes than in dense populations. Although this 'law' has been widely accepted until the 1980s, it has become clear that this scenario was not directly applicable to all populations and plants whose growth scaling is very complex. In other words, the 'law' neglects the plasticity of allocation strategy. Silvertown and Lovett Doust (1993) argued that this rule may be an upper limit of the relationship.

Another suite of empirical results and theoretical deductions comes from agronomy – the 'Law of Constant Final Yield'. This rule deals with size-dependent reproductive allocation in agricultural plant. Total crop biomass increases with density and then levels off, while reproductive output constantly decreases at higher densities. This is explained by the expected pattern according to which plants in competition allocate biomass more in competitive structures and less in reproduction.

All these rules, however, are based on the assumption that population mechanisms contribute to the maintenance of the *status quo* in population dynamics and demography. Numerous ecological and evolutionary models, nevertheless, explore circumstances and mechanisms by which populations do change. As noted by Gurevitch et al. (2002), mean

plant size can be a misleading measurement in models because individual sizes in plants are generally extremely uneven as a consequence of plastic growth in asymmetric competition (Weiner, 1990; Schwinning & Fox, 1995). Largest individuals have disproportionate large negative effects on their small neighbors, since the relative amount of resources that small individuals can acquire is less than what could be expected by their biomass. Among a group of seedlings germinating together, a small advantage in size may confer a large benefit, i.e., progressively greater inequality in competitive abilities over time. Competitive asymmetry, which leads to increased individual variability in size, has been seen as one of the major processes that secure the existence of reproductive individuals, stabilize population dynamics and assure the persistence of populations (Aikio & Pakkasmaa, 2003). Under the assumption that there is a size-threshold for reproduction, asymmetry forces small individuals to decrease in size and to stay below the threshold. Therefore, in the presence of size-dependent mortality and reproduction, only large individuals remain in the population and reproduce, assuring population persistence. On the other hand, under symmetric competition, low variation of individual biomasses increases the possibility that either all individuals remain smaller than the size-threshold for reproduction or that all individuals exceed the threshold. This process may cause strong fluctuations in population size, destabilizes population dynamics (Lomnicki, 1988; Silvertown, 1991; Uchmanski, 2000) and increase the likelihood of extinction due to demographic stochasticity (Ripa & Lundberg 2000). One of the causes of symmetry in competition is genetic relatedness between neighboring individuals. Relatedness reduces size variations either because superior large individuals reduce their resource consumption as an altruistic act towards their smaller relatives, which, now, exceed the size-threshold for reproduction (kin selection; Hamilton, 1964; Maynard-Smith, 1964), or because relatives have similar environmental preferences and genetic uniformity, which result in similar growth rates (Jasienski, 1988; Tonsor, 1989).

All these models are strongly based on the premise that reproductive outcome is a linear function of plant size. Although it is basically true that larger individuals have more seeds, this premise does not allow for the possibility that plastic allometry may change the proportion of resources invested into reproduction. As shown in the study on *L. maculatum* (Stojković et al., 2009), relative allocation to reproductive effort could be enhanced in competition, leading to the decreased effect of asymmetric competition on population dynamics. Also, it was revealed that *L. maculatum* plants grown with genetically identical individuals had higher fitness compared with plants in unrelated patches. It seems that these relations are common for clonal plants (Donohue, 2003). In these genetically structured populations, regulation of population dynamics may include advantageous kin effects. Although there is a possibility that some kin groups may stay bellow the size-threshold for reproduction, the persistence and stability of population size could be assured via selection between kin groups.

4.2 Life-history and population dynamics

Using the logistic model of population growth,

$$\frac{dN}{dt} = rN\left(\frac{K-N}{K}\right)$$

where N is the population size, K is the population's carrying capacity (i.e., the population size at which the per capita birth rate equals the per capita death rate), and r is intrinsic rate of population growth, MacArthur and Wilson (1967) established the 'r / K selection theory'. This theoretical model, integrated with Pianka's concept of the evolution of life-history

strategies (Pianka, 1970, 1974), proposed a relationship between density-dependent population regulation and life-history evolution. In spite of numerous critiques and limited empirical confirmations (see review in Reznick et al., 2002) this model remains one of the most influential theoretical frameworks for understanding life-history evolution. Undoubtedly, adaptive changes of life-history traits are related to the density-dependent adjustment and resource limitation that each population experience. As a consequence, under density-dependent *vs.* density-independent selection individual fitness must be associated with different traits (Boyce, 1984; Mueller, 1997) and evolved life-history strategies should differ between populations facing distinct densities. The organisms in dense populations (i.e., close to the carrying capacity, *K*) are exposed to intense competition and experience density-dependent mortality, which, according to Pianka (1970), determine adaptive life-history changes toward slow development, delayed reproduction, high investment in biomass and greater competitive ability at the cost of low reproductive effort, low fecundity with large investment in each offspring, and high longevity. Contrary, in sparse populations (or populations inhabiting physically variable and unpredictable environments), where mortality factors are mainly density-independent, selection would favor individuals with rapid development, early maturity, high fecundity at the cost of investment in body size, low investment in each offspring, and shorter life span (Pianka, 1970). The later strategy, which is based on selection for traits that enhance population growth rate (*r*), is also expected in a resource-rich, noncompetitive environment.

Although well elaborated argument for life-history strategies as long-term adaptations to the environment in a continuum from pure *r*- to pure *K*-selection, this concept contradicts some basic assumptions about the short-term adaptive responses to competition. In other words, the plasticity of physiological trade-off may oppose long-term microevolutionary trade-offs in a population. For example, fast development is usually assumed to be associated with higher fitness because early hatching/germinated individuals benefit from more available resources compared with subsequent individuals. Also, due to higher possibilities for resource acquirement in a noncompetitive environment, one can expect overall individual performance, i.e., body mass, longevity and total fecundity, to be advanced compared with individuals in a dense population. The question is to what extent a long-term selection can limit the ability of single genotypes to plastically change their allometry strategy in response to environmental variation. Additionally, we may ask what is the consequence of these processes on population dynamics?

In the laboratory evolution experiments on *Acanthoscelides obtectus* two experimental lines were raised for 200 generations. The *r*- and *K*-selected lines were derived by rearing populations at persistently low and high densities, respectively. To test the possibility that plastic responses to the contrasting environmental conditions may oppose long-term life-history strategies established by density-dependent selection, the samples of beetles from both lines were reared for one generation either at their common environment (i.e., low density for the *r*- and high density for the *K*-line) or at the alternate environmental conditions (i.e., low density for the *K*- and high density for the *r*-line). Most of Pianka's predictions on the evolution of life-history strategies under different density conditions were confirmed in *A. obtectus* experimental lines (Stojković & Tucić, unpublished data; but see Tucić et al. (1997) for contrasting results on these experimental lines after only 73 generation of selection). However, preadult life-history traits (i.e., egg size, preadult viability and developmental time) were influenced by short-term density conditions. More importantly, these plastic changes induced by the novel environments (low density for the

K- and high density for the *r*-line) were in opposite directions from the course of selection for life-history traits within experimental lines. Larval experience of *r*- females in dense conditions resulted in significant increase of investment into the egg dimension. This strategy may provide an advantage to offspring in competitive interactions. The short-term relaxation of competition in *K*-line enabled opportune investment into fast offspring development and increase of their viability. These plastic changes in allocation patterns in *K*- experimental line resulted in increase of demographic parameters - intrinsic rate of population growth (*r*) and net reproductive rate (*Ro*). It seems that amplification of per capita amount of resources at low density allowed the enlargement of carrying capacity in the *K*-line and, consequently, enhanced the opportunities for population growth. In population ecology it is well known that offspring born in early life-stages contribute more to the next generation (i.e., to the *r* parameter) than offspring born later. Fertility life tables of *K*-females raised for one generation at low density provided the evidence that the age-specific fecundity schedule was shifted toward earlier days of adulthood with narrow distribution of fecund days (Stojković & Tucić, unpublished data).

The experiment on rice weevil (*Calandra oryzae*) revealed that variations in temperature may change intrinsic rate of population growth (*r*) as a consequence of changes in rate of development, survival and fecundity (Birch, 1948).

Empirical data have provided excellent demonstration on how variation in survival and fecundity, as individuals vary in age, size, fecundity schedule or other life-history characteristics, affects dynamics in population demography.

5. Conclusions

In many ecological models populations are not perceived as being composed of individuals that vary in all aspects of their phenotype. Evolutionary biology is looking for the explanations of evolution and development of various organismal traits, but rarely explores the effects of evolutionary changes on dynamics of populations. The truth is that ecological processes provide the context for evolution, and, also, that changes in individual variability affect all population processes in a continuous feedback manner. Allometry, the study of size-correlated variations in biological form and function, may be seen as a discipline in which both theoretical programs can meet. Allometry investigates how allocation strategies evolved and how they can be changed in respect to the environment and characteristics of populations. Individuals must allocate resources in a way that make the most of their chances for contributing offspring to the next generation while simultaneously maximizing their chance of surviving to reproduce. How organisms manage to solve this complex task depends both on the evolutionary history of a population and on biotic and abiotic conditions at each point of time. Clearly, the dynamic relations between life-histories and growth architecture of organisms and their environments suggest that allometric patterns evolve in response to numerous selection pressures and constraints. At the same time, the way the individual growth and life-histories are shaped in certain environment could largely influence the demographic patterns of a population.

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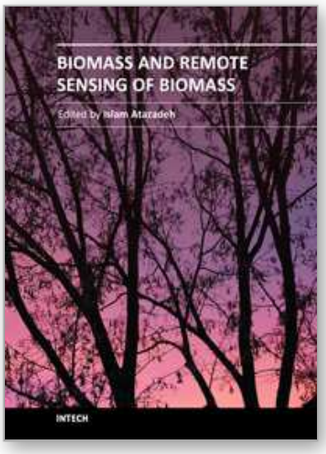

Biomass and Remote Sensing of Biomass

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Generally, the term biomass is used for all materials originating from photosynthesis. However, biomass can equally apply to animals. Conservation and management of biomass is very important. There are various ways and methods for biomass evaluation. One of these methods is remote sensing. Remote sensing provides information about biomass, but also about biodiversity and environmental factors estimation over a wide area. The great potential of remote sensing has received considerable attention over the last few decades in many different areas in biological sciences including nutrient status assessment, weed abundance, deforestation, glacial features in Arctic and Antarctic regions, depth sounding of coastal and ocean depths, and density mapping. The salient features of the book include:
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Use of remote sensing for evaluation of biomass
Evaluation of carbon storage in ecosystems
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