Evolutionary Ecology Research, 2004, **6**: 1107

Introduction

Allocation under multiple resource constraints

In the late 1960s and 1970s, careful thinking about natural selection ultimately led to a revolution in how we think about plant evolutionary ecology and reproductive biology. David Lloyd has been a pioneer and leading figure in this revolution.

In 1992, he suffered a severe infirmity which ended his active academic career (though not his publications!). The following article represents a collaboration that was ongoing at this time but, due to the uncertainty and confusion about David's condition, was shelved. Then, this spring, I was engaged in a conversation with a colleague about the importance of multiple resource constraints on ecological systems generally and mentioned that I had done some theoretical work with David a while back on multiple resource limitation in evolutionary allocation problems, but that it had never been published. Afterwards, I dusted off the old files and was surprised to find an almost finished manuscript that still appeared relevant to ecological questions of current interest. With a bit of work, it led to the following article.

D. Lawrence Venable
University of Arizona

Evolutionary Ecology Research, 2004, **6**: 1109–1121

Allocation under multiple resource constraints

D. Lawrence Venable[1]* and David G. Lloyd[2]

[1]*Department of Ecology and Evolutionary Biology, University of Arizona, Biosciences West, 1041 E. Lowell Street, Tucson, AZ 85721, USA and* [2]*Department of Plant and Microbial Sciences, University of Canterbury, Christchurch, New Zealand*

ABSTRACT

Models of reproductive ecology and life history usually resort to arguments of optimal or ESS allocation of a single limiting resource. Yet real organisms may be limited by multiple resources. We present a verbal-graphical method for analysing allocation problems under multiple resource constraints, focusing on an example of allocation to two structures or functions, subject to two resource constraints. The logic behind this intuitive model is justified by an analytical model, which is applied to a sex allocation example. The evolutionarily stable strategy (ESS) or optimal allocation will usually depend on which constraints are limiting at the ESS. For example, if the carbon : nitrogen ratio required to produce seeds differs from that required to produce pollen, the ESS numbers of seeds and pollen grains will differ depending on which resource is limiting (and take on yet another value if both resources are limiting at the ESS). We show how to determine whether one, the other or both constraints are limiting at the ESS. The degree of difference in the ESS allocation under different constraints is determined by the degree of difference in the ‘resource recipes’ of the structures or functions in question. ESS allocations to structures or functions are predicted to be more sensitive to changes in resource availability when both constraints are limiting than when only one is limiting. In contrast, ESSs are predicted to be more sensitive to changes in fitness equation parameters when one resource is limiting than when both are limiting. Nutrient manipulation experiments are suggested that can test the importance of these ideas. Plastic developmental responses in resource acquisition may result in multiple resource constraints frequently being binding at ESSs. To the degree that resources are substitutable, rather than being required in specific ratios, multiple resource allocation problems can be rephrased as single resource problems.

Keywords: carbon, currency problem, evolutionarily stable strategy, life histories, nitrogen, resource limitation, sex allocation.

INTRODUCTION

It has been suggested that a synthetic approach, combining evolutionary, population and community ecological questions and methodologies with long-term dynamical studies, is leading to a new synthesis in plant ecology (Rees *et al.*, 2001). According to this view, many of the functional constraints on allocation that underlie trade-offs and shape life histories

---

* Author to whom all correspondence should be addressed. e-mail: venable@email.arizona.edu

also affect interspecific interactions, mechanisms of co-existence, succession and community structure (Grubb, 1977; Chesson and Huntly, 1988; Tilman and Pacala, 1993; Venable *et al.*, 1993; Bazzaz, 1996; Turnbull *et al.*, 1999). In recent years, macro-ecological patterns of allocation have been discovered and folded into this emerging synthesis (Niklas and Enquist, 2003). Although it is not always clear which resources are governing allocation decisions, it has become increasingly apparent that multiple resources are involved. Furthermore, their identity and the nature of the limitation have important implications that reverberate throughout ecology (Tilman, 1985; Seastedt and Knapp, 1993; Elser *et al.*, 1996; Huxman *et al.*, 2004).

Models of life-history evolution and reproductive ecology usually rely on cost–benefit analyses of how natural selection favours different patterns of allocation. The cost of various vegetative and reproductive structures and functions has been estimated by measuring dry weight (e.g. Hickman and Pitelka, 1975; Lovett-Doust and Harper, 1980; Cheplick, 1995), by determining nutrient contents (e.g. Chapin, 1989; Ashman, 1994a; Witkowski and Lamont, 1996), by estimating total cumulative carbon allocation from biomass and respiration or other dynamic physiological measures (Reekie and Bazzaz, 1987a; Ashman, 1994b) or by counting meristems (Watson, 1984; Geber, 1990; Duffy *et al.*, 1999). In studies where more than one resource has been measured, different proportions have been found for different resources (e.g. Abrahamson and Caswell, 1982; Chapin, 1989; Carroll and Delph, 1996; Hemborg and Karlsson, 1999; Henery and Westoby, 2001), leading to a debate as to which currency is the most appropriate for analysing life history and reproductive strategies.

It is generally agreed that the appropriate currency is the one that is actually limiting fitness (Lovett-Doust, 1989; Stanton and Galloway, 1990), yet many complications may occur. Different structures or functions may have different resource requirements and be limited by different resources. For example, pollen has more protein per gram than seed in many grasses and crucifers, though in *Pinus* pollen has less protein than seed (Goldman and Willson, 1986). More than one resource may be simultaneously limiting, different resources may be limiting at different naturally occurring resource levels, and evolutionary or plastic shifts in allocation may result in a shift from limitation by one resource to another.

Most life-history and reproductive allocation models have either explicitly or implicitly assumed that growth and reproduction are limited by a single resource, usually energy, time or just ‘expenditure’ (e.g. Fisher, 1930; Charnov, 1982). McGinley and Charnov (1989) have considered a two-resource model of offspring size and number which assumes that resources will be utilized in proportion to their availability. Since offspring size–number models usually consider only a single structure – offspring – many of the problems related to differential resource use and the possibility of limitation by different resources at different times can be avoided. We have considered some of the general properties of allocation models with single and multiple constraints (Lloyd and Venable, 1992). The techniques we discussed there explicitly treat resource constraints and are readily applicable to resource allocation problems with multiple resource constraints.

In what follows, we model the allocation of two resources to two structures or functions which may require them in specific proportions. This is the simplest case to understand and is readily generalizable to more than two resources or structures. First, we present an intuitive verbal-graphical model of the problem, then a more rigorous analytical treatment. Finally, we illustrate the general approach with a gender allocation problem for a co-sexual organism with non-linear fitness gain curves that is potentially limited by two resources.

THE MODEL

We consider allocation to two structures or functions that may require differing amounts of a limited supply of two complementary resources – that is, resources that must be utilized in certain proportions to make the structures or perform the functions of interest. We call the resources 'carbon' and 'nitrogen' for the sake of concreteness. Let x_1 and x_2 be the 'amounts' of structures 1 and 2 (e.g. the numbers of seeds and pollen grains) produced by an organism (for convenience we treat these amounts as continuous variables). Let $[C_i, N_i]$ be the 'resource recipe' for making structure i; for example, C_1 carbon units and N_1 nitrogen units are required to make one seed. Implicit in this formulation is that the recipe may vary for different structures. Finally, let C_A and N_A be the amounts of the two resources available to the plant. The resource constraints are that the 'carbon' utilized must be less than or equal to the carbon available ($x_1C_1 + x_2C_2 \leq C_A$) and that the 'nitrogen' utilized must be less than or equal to the nitrogen available ($x_1N_1 + x_2N_2 \leq N_A$).

The verbal-graphical model

A number of aspects of the general problem can be readily seen from a plot of the resource constraints on the x_1, x_2 axes. With reference to Fig. 1, the feasible allocations to the two structures are given by the shaded area to the lower left of both resource constraint lines (allocations above and to the right of either line would require more than the available amount of resources). Note that the model assumptions from the previous paragraph result in the constraints being straight lines (though our results generalize readily to non-linear cost functions). The x_1 and x_2 intercepts are the maximum numbers of each structure that could be produced if all of the available limiting resource were allocated to only one of the two structures (i.e. the amount of the limiting resource available divided by the amount needed to make each seed or pollen grain).

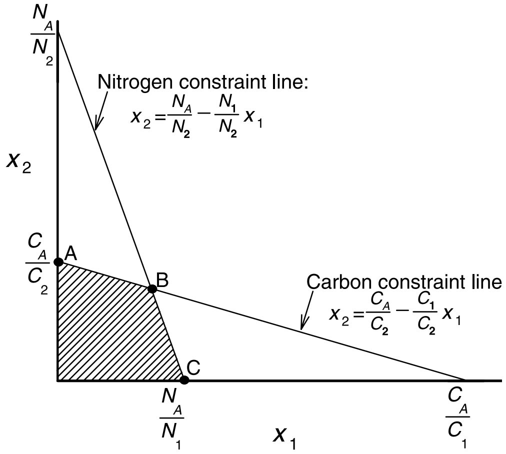

Fig. 1. Plot of two resource constraints (here called 'nitrogen' and 'carbon') on axes of the number or amount of two structures or functions, x_1 and x_2.. The resource constraints specify that the carbon utilized must be less than or equal to the carbon available ($x_1C_1 + x_2C_2 \leq C_A$) and that the nitrogen utilized must be less than or equal to the nitrogen available ($x_1N_1 + x_2N_2 \leq N_A$). The shaded area contains the feasible allocations satisfying these constraints.

The 'resource recipes' determine the slopes of the two constraint lines (C_1/C_2 and N_1/N_2), while the resource availabilities determine how far out from the origin the constraint lines are (adding more of a resource would move its constraint line out from the origin without changing the slope). In Figs. 1–3, structure 1 is relatively more expensive in nitrogen and less expensive in carbon than structure 2, since the nitrogen line is drawn steeper than the carbon line ($N_1/N_2 > C_1/C_2$). Since the nitrogen constraint has a higher intercept on the x_2 axis, the plant would run out of carbon before it ran out of nitrogen if it attempted to make only structures of type 2 (e.g. pollen grains). Conversely, since the carbon constraint line has a higher x_1 intercept, the plant would run out of nitrogen first if it tried to make only structures of type 1 (e.g. seeds). A particular allocation is represented by a point on the graph and can be thought of in two ways. The relative allocation to the two structures measured in units of the number or amount of the structures (x_2/x_1) is the slope of a straight line from the origin to the point (x_1, x_2) representing the allocation. Relative allocation can also be expressed as the proportion of a limiting resource allocated to a particular structure or function (e.g. c_2x_2/c_1x_1 for carbon). The geometric interpretation of the proportion of a limiting resource is the proportion of the length of the constraint line (between its two intercepts) that lies on either side of the point representing that allocation. For example, a 50 : 50 allocation of the available carbon is represented by the point ($C_A/2C_1$, $C_A/2C_2$) that bisects the line representing the carbon constraint.

The simplest case of the two-structure, two-complementary resources problem occurs when the constraint lines for the two resources do not cross. If they do not, then the constraint line for the over-abundant resource lies completely outside the zone of feasible allocations, and only the inner constraint is limiting for any feasible allocation. The 'resource recipes' for structures and the amounts of resource available determine whether or not the constraint lines cross. Since we have modelled straight line constraints, the condition for not crossing can be stated simply in terms of the intercepts: if $C_A/C_1 < N_A/N_1$ and $C_A/N_2 < N_A/N_2$, then only carbon can be limiting, or, if the inequalities are reversed, only nitrogen can be limiting. Once it is determined that the lines do not cross and which resource is limiting, the ESS for the particular problem at hand can be determined using the standard techniques for two structures and one limiting resource (Chaing, 1984; Vincent and Brown, 1988; Venable, 1992; see the sex allocation example below).

If the constraint lines cross as in Fig.1, some of the feasible allocations that are candidates for an evolutionarily stable strategy (ESS) would then result in carbon being the limiting resource (line segment [AB]), some would result in nitrogen being limiting (line segment [BC]), and at one allocation (at point B) either or both resources may be limiting.

A simple graphical way to determine which of these situations is occurring relies on the interpretation of allocation as the distance along a resource constraint between the x_1 and x_2 intercepts. The technique involves first determining the single-resource ESS allocation using standard single-resource procedures. Then this single-resource ESS is plotted on each resource constraint as if working with a single-resource problem (e.g. if the single-resource ESS allocation were, say, 0.2, the point one-fifth of the way down each constraint line would be plotted [Fig. 2a]). If the single-resource ESS allocation for either resource lies on the feasible portion of the relevant constraint line (e.g. carbon in Fig. 2a), that point is the two-resource ESS (there is never more than one resource for which the single-resource ESS lies on the feasible portion of the constraint lines). This procedure also identifies the limiting resource. If, however, both single-resource ESSs lie on the unfeasible portions

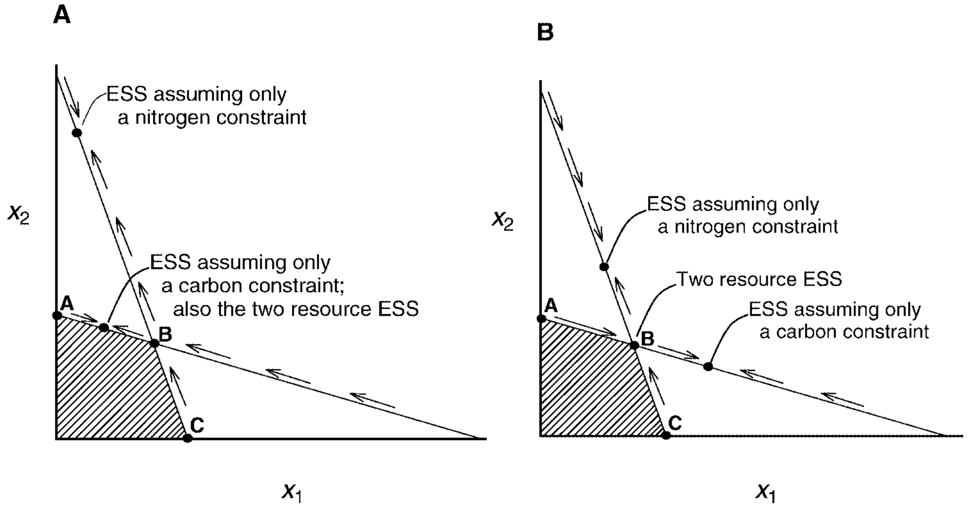

Fig. 2. The nature of the ESS when one or both resource constraints are binding is shown on a plot of two resource constraints ('nitrogen' and 'carbon') where the axes are the number or amount of two structures or functions, x_1 and x_2. (A) This situation shows an arbitrary ESS, which, under the assumption of only a nitrogen constraint, lies outside the two-constraint feasible area (shaded). Assuming only a carbon constraint, this same arbitrary ESS lies on the line segment [A, B], which is on the border of the shaded area of feasible allocations. In such cases, the feasible single-constraint ESS (carbon in this case) is the two-resources ESS. (B) When the ESS is outside the feasible area when either a carbon or a nitrogen constraint is assumed to apply, the ESS will be at B, where the constraint lines intersect. Arrows show the direction in which selection will try to move the allocation strategy along each constraint line (selection gradients).

of the constraint lines (e.g. Fig. 2b), the two-resource ESS lies at point B, the intersection of the constraint lines, and both resources are limiting.

The intuition behind this graphical solution can be seen by imagining a population with an arbitrary initial resource allocation (e.g. point B) and analysing whether selection favours a shift in allocation, and if so in what direction. Selection for use of a limiting-resource favours a shift in allocation towards that resource's single-resource ESS (arrows in Fig. 2). If that ESS is on the feasible segment of the resource constraint at a point other than B, evolution towards it results in utilization of less than the limiting amount of the other resource. Since the second resource is not limiting, selection moves the population to the feasible single-limiting-resource ESS (Fig. 2a). If, however, neither single-resource ESS is on the feasible segment, then selection on a population at B favours infeasible changes. Selection on populations at feasible allocations other than B favours movement towards the single-resource ESSs, which, in this case, means towards B (Fig. 2b). This logic can be formalized mathematically as follows.

The mathematical justification of the graphical model

We first focus on the general problem of determining which resource is limiting for any allocation problem, and then solve, as an example, a sex allocation problem for a co-sexual organism with non-linear fitness gain curves described by power functions. We will assume that there is a unique global single-strategy ESS for our general discussion (this is true for the example we analyse).

Let fitness be described by some function $W(x_1, x_2)$. If we imagine graphing $W(x_1, x_2)$ as a third axis moving out from the paper in Fig. 1, we can construct an adaptive landscape in which fitness is plotted as a function of the numbers of the two types of structures, x_1 and x_2. In frequency-dependent problems, such as gender allocation, the shape of the landscape will shift as the frequencies of allocation strategies shift. Contour lines on the two-dimensional (x_1, x_2) projection of this fitness topography represent allocations of equal fitness (Fig. 3). Feasible strategies still occur in the hatched area of Fig. 3, thus the problem is to find the ESS on this shifting topography subject to the two resource constraints.

In principle, the ESS occurs at a point on the line segment ABC which is tangent to an equal-fitness contour when the rest of the population also has this allocation (Brown and Venable, 1986; Lloyd and Venable, 1992). The possible exception is at point B, which is a non-differentiable point or 'kink' along ABC at which no slope can be evaluated. In what follows, we deal with first-order necessary conditions. To ensure that any solutions are unique global ESSs, we must also ascertain that the solution obtained is not a minimum, saddle point or local ESS.

We have adopted the convention of calling the steeper constraint the 'nitrogen constraint', so in all of the following arguments it is assumed that $N_1/N_2 > C_1/C_2$. We can determine whether the ESS is along [AB], [BC] or at B by comparing the slope of the equal fitness contour passing through point B (assuming the population allocation is at point B also) with the slopes of the two resource constraints. If the slope of the equal fitness

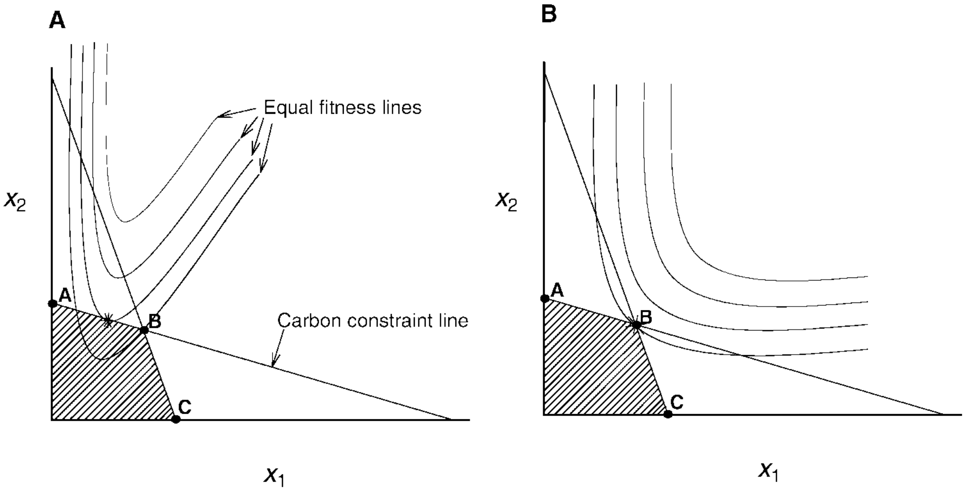

Fig. 3. Contours representing equal fitness values are plotted together with the constraints for the state space explained in Fig. 1. Successive contours moving towards the top and right have progressively higher fitness. Whether the ESS lies along [A, B], [B, C] or is at B can be determined by evaluating the slope at B of the equal fitness line passing through B. (A) When that slope is greater than that of the carbon constraint (i.e. the constraint with greatest slope), only that constraint will be limiting and the ESS will be along [A, B]. (B) When the slope at B of the equal fitness line passing through B is less than that of the constraint with greatest slope, but greater than that of the constraint with the lowest slope, the ESS will be at B.

contour at B is greater than the slope of the carbon constraint, then there must be another equal fitness line of higher fitness that intersects [AB] to the left of B (Fig. 3a). Thus a population with allocation B is subject to invasion by mutants somewhere on [AB] that will have higher fitness than individuals with allocation B. Any ESS will occur along [AB], and carbon is the only limiting resource (note that this also implies that the single-resource ESS for carbon must lie to the left of B). Similarly, if the slope of the equal fitness line passing through B with the population allocation also at B is less than (more steep than) the slope of the nitrogen constraint, then the ESS will lie on [BC] and nitrogen is the only limiting resource (the single-resource ESS for nitrogen would also lie on [BC]). If the slope of the equal fitness line passing through B (when the population allocation is B) is steeper than the slope of the carbon constraint and shallower than the slope of the nitrogen constraint, then all allocations along [AB] or [BC] have lower fitness than B and thus cannot invade. B is the ESS, and both resources are limiting (Fig. 3b). This situation implies that both single-resource ESSs would lie along the portions of the constraint lines that are unattainable in the two-resource problem. The slopes of the constraint lines are ratios of the resource recipes and, by the implicit function rule, the slope of equal fitness lines in Fig. 3 equals

$$-\frac{\partial W}{\partial x_1}\bigg/\frac{\partial W}{\partial x_2} \tag{1}$$

Thus carbon alone is limiting if

$$\left.\frac{\partial W}{\partial x_1}\bigg/\frac{\partial W}{\partial x_2}\right|_B < \frac{C_1}{C_2} \tag{2}$$

Nitrogen alone is limiting if

$$\left.\frac{\partial W}{\partial x_1}\bigg/\frac{\partial W}{\partial x_2}\right|_B > \frac{N_1}{N_2} \tag{3}$$

Both resources are limiting if both of these inequalities are reversed (in the unlikely case of an equality in one of these expressions, one resource would be completely utilized, but not limiting in the sense that any increment would not be utilized). When both resources are limiting, the ESS is at point B, which can be calculated as the simultaneous solution to the carbon and nitrogen constraint equations without recourse to the fitness equation:

$$x_1^* = \frac{C_A N_1 - C_1 N_A}{C_2 N_1 - C_1 N_2} \qquad x_2^* = \frac{C_A N_2 - N_A C_2}{C_1 N_2 - N_1 C_2} \tag{4}$$

These conditions can alternatively be derived from an analysis of the fitness and constraint gradients at point B.

We have assumed throughout this paper that constraint lines and cost functions are linear. While this was done for didactic simplicity, the model could be generalized to non-linear cost functions (though this is beyond our current scope). Briefly, additional structures could require progressively more of a resource (diminishing returns scenario) or progressively less resource (economy of scale or fixed initial cost scenario). This might be due, for example, to needing progressively more (or less) expensive auxiliary structures as more seeds are produced. A diminishing returns scenario would result in convex constraint lines (bowing out), while an economy of scale scenario would result in concave constraint lines (bowing in towards the origin). The main arguments and conclusions made here would still apply. However, since the slopes of the constraints would not be constant, they would need to be evaluated at the intersection, B. Also, ESSs would tend to shift away from structures or functions with diminishing returns cost functions and towards those with fixed initial costs. A general treatment of ESSs with non-linear cost functions for single-constraint problems is given in Venable (1996).

Sex allocation for a co-sexual organism with two limiting resources

As a concrete example we solve a sex allocation problem for a co-sexual organism experiencing non-linear fitness gain curves. Let the fitness of a mutant co-sexual individual within a co-sexual resident population be described by

$$W_m = x_{1m}^{\;z} + \frac{x_{2m}^{\;y}}{Kx_{2R}^{\;y}} \cdot Kx_{1R}^{\;z} \tag{5}$$

where resident and mutant terms are indicated by the *m* and *R* subscripts. Female fitness of the mutant is a power function of the number of seeds produced by the mutant, $x_{1m}^{\;z}$. Male fitness of the mutant (the number of seeds fathered) is a product of two terms: (1) the proportion of the total population pollen success that is the mutant's (pollen success is assumed to be a power function of the number of pollen grains produced), and (2) the total seed fitness of the population. The first term of male fitness is given by $x_{2m}^{\;y}/Kx_{2R}^{\;y}$, where K is the population size. The total seed fitness of the population is given by $x_{1R}^{\;z}K$. Other constants that do not affect the solution are frequently included for completeness (e.g. Lloyd, 1984). To ensure that the following first-order conditions lead to a unique global ESS, we assume that $y + z > 2yz$ (cf. Lloyd, 1984). To calculate the slope of the equal fitness lines of Fig. 3, the partial derivatives with respect to the mutant strategies are:

$$\begin{aligned} \frac{\partial W_m}{\partial x_{1m}} &= Zx_{1m}^{\;z-1} \\ \frac{\partial W_m}{\partial x_{2m}} &= \frac{yx_{2m}^{\;y-1}x_{1R}^{\;z}}{x_{2R}^{\;y}} \end{aligned} \tag{6}$$

Setting the mutant and resident strategies equal and calculating (1) gives $-zx_2/yx_1$. Thus, using the rules developed in the previous section, if $\left.\frac{zx_2}{yx_1}\right|_B < \frac{C_1}{C_2}$, then only carbon is limiting. If $\left.\frac{zx_2}{yx_1}\right|_B > \frac{N_1}{N_2}$, then only nitrogen is limiting. If these inequalities are reversed, then both resources are limiting and the intersection of the constraint lines, B, is the ESS. These inequalities can be rearranged as

$$\left.\frac{C_1x_1}{C_2x_2}\right|_B > \frac{z}{y} \quad \text{and} \quad \left.\frac{N_1x_1}{N_2x_2}\right|_B < \frac{z}{y}$$

This means that if the ratio of carbon allocation to seeds (C_1x_1) over carbon allocation to pollen (C_2x_2) at point B is greater than z/y, then only carbon is limiting. Similarly, if the ratio of nitrogen allocated to seeds over nitrogen allocated to pollen is less than z/y, then only nitrogen is limiting.

Below we use the technique of Lagrange multipliers to show that z/y is the ESS allocation of carbon when only carbon is limiting. This technique is used for optimization subject to constraint. It involves writing down a Lagrange function, which brings the constraint into the equation to be maximized (Chiang, 1984; Venable, 1992). The Lagrange function for the case when only carbon is limiting is:

$$L = x_{1m}{}^{z} + \frac{x_{1R}{}^{z} x_{2m}{}^{y}}{x_{2R}{}^{y}} + \lambda_c (C_A - x_{1m}C_1 - x_{2m}C_2) \tag{7}$$

The ESS for this case can be calculated as follows:

$$\frac{\partial L}{\partial x_{1m}} = z x^{*}_{1m}{}^{z-1} - \lambda_c C_1 = 0 \tag{8}$$

$$\frac{\partial L}{\partial x_{2m}} = \frac{y x_{1R}{}^{z} x^{*}_{2m}{}^{y-1}}{x_{2R}{}^{y}} - \lambda_c C_2 = 0 \tag{9}$$

$$\frac{\partial L}{\partial \lambda} = C_A - x^{*}_{1m}C_1 - x^{*}_{2m}C_2 = 0 \tag{10}$$

$$\frac{z x_1^{*\,z-1}}{C_1} = \frac{y x_1^{*\,z}}{x_2^{*} C_2} \Rightarrow \frac{x_1^{*} C_1}{x_2^{*} C_2} = \frac{z}{y} \tag{11}$$

$$x_1^{*} = \frac{z}{y+z}\frac{C_A}{C_1};\; x_2^{*} = \frac{y}{y+z}\frac{C_A}{C_2} \tag{12}$$

Remember from Fig. 1 that C_A/C_1 and C_A/C_2 are the number of seeds and pollen grains, respectively, that could be produced if all carbon was allocated to seeds or all to pollen. Thus the results indicate that the ESS is to allocate the available carbon in the proportion z/y to each function. Recall that we adopted the convention that seeds (structure 1) are relatively more expensive in nitrogen and less expensive in carbon than pollen (structure 2), drawing the nitrogen line steeper than the carbon line ($N_1/N_2 > C_1/C_2$). Referring back to the conditions for limitation by carbon only, we now see that they can be read as 'carbon alone will be limiting if the proportion of carbon allocated to seeds at the carbon limited ESS (z/y) is less than the proportion of carbon allocated to seeds at B, $\left.\frac{C_1 x_1}{C_2 x_2}\right|_B$'. The intuition behind this is that if the proportion of carbon allocated to seeds at the carbon limited ESS were greater than that at B, the ESS would occur on the unattainable part of the carbon constraint line where nitrogen is limiting, but if it is less it occurs along segment [AB] where carbon is limiting and nitrogen is not. This is an analytical derivation for this example of our verbal-graphical condition that if the single-resource ESS for carbon lies to the left of B (in Fig. 2a), then carbon will be the only limiting resource.

If nitrogen is limiting, a similar procedure shows that the ESS is to make the number of pollen grains and seeds that allocates available nitrogen in a z/y ratio. If both resources are limiting, the ESS is at B, the formula for which was given above.

While the allocation ratio of 'expenditure' is the same whether carbon or nitrogen is limiting, the ESS ratio of seeds to pollen is not (unless they happen to have the same resource recipe). The ESS ratio of seeds to pollen under carbon limitation is $x_1^*/x_2^* = z/y \cdot C_2/C_1$, while under nitrogen limitation it is $x_1^*/x_2^* = z/y \cdot N_2/N_1$. Thus unless the carbon : nitrogen ratio required to produce seeds is the same as that required to produce pollen, the ESS numbers of seeds and pollen grains differ depending on which resource is limiting. The ESS when both resources are limiting is again different, and does not even contain the diminishing return exponents y and z.

DISCUSSION

According to our model, multiple-resource problems often reduce to single-resource problems. However, one must first determine which resource is limiting, because the ESS allocation to structures or functions will usually vary depending on which resource is limiting. Also, it is possible for more than one resource to be limiting at the ESS, in which case the ESS allocation will be different from either of the single limiting resource ESSs. Both graphical and analytic procedures have been outlined for determining which of these three situations pertains for a two-structure, two-resource model and procedures for determining the ESS have been presented. As an example, the problem of gender allocation for co-sexual plant species limited by two nutrients has been developed.

A number of predictions can be made with regard to resource addition experiments. The ESS relative allocation to different structures (x_1/x_2) will vary depending on which resource is limiting, with the magnitude of the difference depending on how different the resource recipes are for the two structures. For example, in the co-sex gender allocation example, the ESS allocation ratio to genders equalled $z/y \cdot C_2/C_1$ under carbon limitation but $z/y \cdot N_2/N_1$ under nitrogen limitation, and thus differs by an amount determined by the difference between C_2/C_1 and N_2/N_1. For homothetic fitness functions such as the one in this example, these single-constraint ESSs will represent the extremes of allocation ratios ('homothetic functions' is a more general category of functions than 'homogeneous functions' for which the single-resource ESS allocation ratio does not vary with the amount of resource present; see Chaing, 1984, for a mathematical definition). A plant limited by only one resource will not initially change its relative allocation when the limited resource is supplemented (i.e. when its resource constraint line is elevated, maintaining the same slope). More of both structures will be produced in the same ratio. However, with further increments of the limiting resource, eventually a second resource will also become limiting and the ESS (at B) will begin to shift gradually towards the single-resource ESS for the other resource. Eventually, if enough of the first resource is added, it will no longer be limiting and further addition will result in no change in either the number or relative allocation to the two structures. Thus, if this model is correct, allocation responses of plants grown at different resources levels can determine whether one, the other or both resources are limiting, based on the different expected plant behaviours in these three cases. Tests of the model could be constructed by measuring allocation shifts to varying nutrient levels for different plants with high versus low divergence in resource recipes.

A quite different model behaviour results if, rather than changing resource availabilities, the curvature of the fitness gain curves is changed (i.e. the rate of diminishing returns from allocation to a particular structure or function). When only one resource is limiting, the ESS changes in response to changes in curvature of the fitness gain curves. Yet, when two resources are limiting, the ESS will not change in response to changes in the curvature of the fitness gain curves. For example, in the gender allocation problem, changing y or z changes the ESS under carbon or nitrogen limitation, but if both are limiting, the ESS is at point B and changing y or z does not change the ESS. This is the opposite of what happens when changing resource levels, where the ESS tends not to change in response to nutrient addition when only one resource is limiting, but changes when both resources are limiting. Thus, if only one resource is limiting, the ESS is more sensitive to changes in the underlying fitness formula. If both resources are limiting, it is more sensitive to differences in resource availability. The arguments presented here tend to negate the idea that carbon integrates the allocation patterns of other nutrients and therefore makes a suitable single currency to assess allocation patterns (Reekie and Bazzaz, 1987b).

Ecophysiological theory suggests that plants make plastic and evolutionary homeostatic adjustments, such as changes in the root : shoot ratio, that tend to increase the acquisition of limiting resources at the expense of acquiring those available in superabundance (Bloom *et al.*, 1985). To the extent that such mechanisms are successful at balancing resource capture, we should find that plants are frequently at ESSs limited by multiple resources. Thus, plants may frequently occur in the state space where ESS allocations shift with changes in resource availability. An analogous argument has been made in the sex allocation literature that selection will favour simultaneous pollen and resource limitation (Haig and Westoby, 1988).

Another possibility not treated in our model is that plants may vary the composition of organs depending on resource availability. This would mean that resources are somewhat substitutable as implied by McGinley and Charnov (1989). At one extreme, the model's predictions should be approximately right even if plants vary composition with availability if the additional 'non-limiting' resource has a minimal impact on fitness. At the other extreme, if resources are truly substitutable, an exchange rate should be calculable and the two resource-problem reduces to a single-resource problem.

Explicit treatment of multiple resources, as we have outlined in this paper, adds a new dimension to the predictions of allocation models. This provides an additional level of realism that may be quite useful for understanding plant life histories *per se* and ultimately for understanding the broader ecological implications of multiple resources and allocation decisions (Rees *et al.*, 2001).

REFERENCES

Abrahamson, W.G. and Caswell, H. 1982. On the comparative allocation of biomass, energy, and nutrients in plants. *Ecology*, **63**: 982–991.

Ashman, T.L. 1994a. A dynamic perspective on the physiological cost of reproduction in plants. *Am. Nat.*, **144**: 300–316.

Ashman, T.L. 1994b. Reproductive allocation in hermaphrodite and female plants of *Sidalcea oregano* ssp. *spicata* (Malvaceae) using 4 currencies. *Am. J. Bot.*, **81**: 433–438.

Bazzaz, F.A. 1996. *Plants in Changing Environments*. Cambridge: Cambridge University Press.

Bloom, A.J., Chapin, F.S. and Mooney, H.A. 1985. Resource limitation in plants: an economic analogy. *Annu. Rev. Ecol. Syst.*, **16**: 363–392.

Brown, J.S. and Venable, D.L. 1986. Evolutionary ecology of seed-bank annuals in temporally varying environments. *Am. Nat.*, **127**: 31–47.

Carroll, S.B. and Delph, L.F. 1996. The effects of gender and plant architecture on allocation to flowers in dioecious *Silene latifolia* (Caryophyllaceae). *Int. J. Plant Sci.*, **157**: 493–500.

Chaing, A.C. 1984. *Fundamental Methods of Mathematical Economics*, 3rd edn. New York: McGraw-Hill.

Chapin, F.S. 1989. The cost of tundra plant structures: evaluation of concepts and currencies. *Am. Nat.*, **133**: 1–19.

Charnov, E.L. 1982. *The Theory of Sex Allocation*. Princeton, NJ: Princeton University Press.

Cheplick, G.P. 1995. Life-history trade-offs in *Amphibromus scabrivalvis* (Poaceae) – allocation to clonal growth, storage, and cleistogamous reproduction. *Am. J. Bot.*, **82**: 621–629.

Chesson, P.L. and Huntly, N. 1988. Community consequences of life-history traits in a variable environment. *Ann. Zool. Fenn.*, **25**: 5–16.

Duffy, N.M., Bonser, S.P. and Aarssen, L.W. 1999. Patterns of variation in meristem allocation across genotypes and species in monocarpic Brassicaceae. *Oikos*, **84**: 284–292.

Elser J.J., Dobberfuhl, D.R., MacKay, N.A. and Schampel, J.H. 1996. Organism size, life history, and N : P stoichiometry. *Bioscience*, **46**: 674–684.

Fisher, R.A. 1930. *The Genetical Theory of Natural Selection*. Oxford: Clarendon Press.

Geber, M.A. 1990. The cost of meristem limitation in *Polygonum arenastrum* – negative genetic correlations between fecundity and growth. *Evolution*, **44**: 799–819.

Goldman, D.A. and Willson, M.F. 1986. Sex allocation in functionally hermaphroditic plants: a review and critique. *Bot. Rev.*, **52**: 157–194.

Grubb, P.J. 1977. Maintenance of species-richness in plant communities – importance of regeneration niche. *Biol. Rev. Camb. Phil. Soc.*, **52**: 107–145.

Haig, D. and Westoby, M. 1988. On limits to seed reproduction. *Am. Nat.*, **131**: 757–759.

Hemborg, A.M. and Karlsson, P.S. 1999. Sexual differences in biomass and nutrient allocation of first-year *Silene dioica* plants. *Oecologia*, **118**: 453–460.

Henery, M.L. and. Westoby, M. 2001. Seed mass and seed nutrient content as predictors of seed output variation between species. *Oikos*, **92**: 479–490

Hickman, J.C. and Pitelka, L.F. 1975. Dry weight indicates energy allocation in ecological strategy analysis of plants. *Oecologia* (*Berl.*), **21**: 117–121.

Huxman T.E., Smith, M.D., Fay, P.A. *et al.* 2004. Convergence across biomes to a common rain-use efficiency. *Nature*, **429**: 651–654.

Lloyd, D.G. 1984. Gender allocations in outcrossing cosexual plants. In *Principles of Plant Population Ecology* (R. Dirzo and J. Sarukhan, eds.), pp. 277–300. Sunderland, MA: Sinauer Associates.

Lloyd, D.G. and Venable, D.L. 1992. Some properties of phenotypic models of natural selection with single and multiple constraints. *Theor. Pop. Biol.*, **41**: 90–110.

Lovett-Doust, J. 1989. Plant reproductive strategies and resource allocation. *TREE*, **4**: 230–234.

Lovett-Doust, J. and Harper, J.L. 1980. The resource costs of gender and maternal support in an andromonoecious umbellifer, *Smyrniuolusatrum* L. *New Phytol.*, **85**: 251–264.

McGinley, M.A. and Charnov, E.L. 1989. Multiple resources and the optimal balance between size and number of offspring. *Evol. Ecol.*, **2**: 77–84.

Niklas, K.J. and Enquist, B.J. 2003 An allometric model for seed plant reproduction. *Evol. Ecol. Res.*, **5**: 79–88.

Reekie, E.G. and Bazzaz, F.A. 1987a. Reproductive effort in plants. 1. Carbon allocation to reproduction. *Am. Nat.*, **129**: 876–896.

Reekie, E.G. and Bazzaz, F.A. 1987b. Reproductive effort in plants. 2. Does carbon reflect the allocation of other resources? *Am. Nat.*, **129**: 897–906.

Rees, M., Condit, R., Crawley, M., Pacala, S. and Tilman, D. 2001. Long-term studies of vegetation dynamics. *Science*, **293**: 650–655.

Seastedt, T.R. and Knapp, A.K. 1993. Consequences of nonequilibrium resource availability across multiple time scales: the transient maxima hypothesis. *Am. Nat.*, **141**: 621–633.

Stanton, M.L. and Galloway, L.F. 1990. Natural selection and allocation to reproduction in flowering plants. In *Sex Allocation and Sex Change: Experiments and Models* (M. Mangel, ed.), pp. 1–50. Providence, RI: American Mathematical Society.

Tilman, D. 1985. The resource-ratio hypothesis of plant succession. *Am. Nat.*, **125**: 827–852.

Tilman, D. and Pacala, S. 1993. Species coexistence mechanisms in plants. In *Species Diversity in Ecological Communities* (R.E. Ricklefs and D. Schluter, eds.), pp. 13–25. Chicago, IL: University of Chicago Press.

Turnbull, L.A., Rees, M. and Crawley, M.J. 1999. Seed mass and the competition/colonization trade-off: a sowing experiment. *J. Ecol.*, **87**: 899–912.

Venable, D.L. 1992. Size–number trade-offs and the variation of seed size with plant resource status. *Am. Nat.*, **140**: 287–304.

Venable, D.L. 1996. Packaging and provisioning in plant reproduction. *Phil. Trans. R. Soc. Lond. B*, **351**: 1319–1329.

Venable, D.L., Pake, C.E. and Caprio, A.C. 1993. Diversity and coexistence of Sonoran desert winter annuals. *Plant Spec. Biol.*, **8**: 207–216.

Vincent, T.L. and Brown, J.S. 1988. The evolution of ESS theory. *ARES*, **19**: 423–443.

Watson, M.A. 1984. Developmental constraints: effect on population growth and pattern of resource allocation in a clonal plant. *Am. Nat.*, **123**: 411–426.

Witkowski, E.T.F. and Lamont, B.B. 1996. Disproportionate allocation of mineral nutrients and carbon between vegetative and reproductive structures in *Banksia hookeriana. Oecologia*, **105**: 38–42.