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The quantitative assessment of the benefits of physiological integration in clonal plants

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ABSTRACT

A genet of a clonal plant often has ramets persistently interconnected by living tissue capable of supporting the exchange of materials. This condition is known as physiological integration. A quantitative framework is developed for the study of the fitness benefits of physiological integration in clonal plants in spatially heterogeneous environments. We argue that the relative growth rate of the genet is a suitable approximate measure of fitness. Fitness benefits of physiological integration are then measured by comparing genet relative growth rates between heterogeneous and homogeneous environmental conditions. Fitness benefit measures are derived for both exponential and non-exponential growth of genet (clonal) fragments and for equilibrium scenarios. For short time-scales and equilibrium scenarios, we show how the fitness benefit (at the level of the genet) can be decomposed into net benefits accruing at the level of the genet fragment, which can then be further analysed in terms of costs and benefits for the parent and offspring sections of a genet fragment. Applying these benefit measures to simple models of clonal plant growth shows that net benefits of physiological integration may disappear with time and become net costs when physiological integration occurs between strictly good and poor environments. Such time dependence is predicted to result from long-term dominance of total genet growth by genet fragments in good environments. Time dependence, however, would not necessarily occur when the various environments are not strictly good or bad but have complementary attributes. Similarly, net benefits would not necessarily be time-dependent under equilibrium growth scenarios. The net benefit measures derived here allow such time dependence to be assessed in an experimental setting. Although the quantitative methods developed here focus specifically on a common experimental design in which genet fragments are divided into sections subject to different environmental conditions, these methods extend to complex scenarios that might be justified by particular circumstances in the field.

Keywords: fitness, non-linear averaging, paired-section experiment, physiological integration, relative growth rate, spatial heterogeneity.

INTRODUCTION

The clonal growth pattern of many herbaceous perennial plants means that the genetic individual (i.e. the genet) consists of collections of ramets interconnected by persistent

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rhizomes or stolons. Such connections lead to the possibility of the exchange of materials between ramets – in other words, physiological integration. One role of physiological continuity is the support of new ramets by parent ramets during establishment. However, the common maintenance of connections beyond establishment suggests some longer-term benefits (see Jónsdóttir and Watson, 1997, and references therein). One possible benefit is the buffering of spatial variation in the conditions for further growth of established parts of a clone. Indeed, physiological integration may be included among other life-history traits, such as seed dispersal, seed dormancy, seed heteromorphisms, flower longevity and sexual dimorphism, which have been hypothesized to provide fitness benefits to plants in a variable environment (Venable and Brown, 1988; Cipollini and Stiles, 1991; Portnoy and Willson, 1993; Ashman and Schoen, 1994; Heschel and Paige, 1995; Izhaki *et al.*, 1995; Nakashizuka *et al.*, 1995; Hyatt and Evans, 1998; Wenny and Levey, 1998).

Spatial variation in the conditions for plant growth may occur on scales of ramets or small collections of ramets. For example, large variation over spatial scales of tens of centimetres or less can occur in soil moisture (Kelly and Canham, 1992; Ryel *et al.*, 1996), mineral nutrients (Hook *et al.*, 1991; Afzal and Adams, 1992; Kelly and Canham, 1992; Jackson and Caldwell, 1993a,b; Ryel *et al.*, 1996; Derner *et al.*, 1997), light (Kelly and Canham, 1992; Tang and Washitani, 1995), space (Tang and Washitani, 1995) and salinity (Salzman and Parker, 1985). In the presence of physiological integration, ramets or collections of ramets may be supported for a time by materials supplied through connections to neighbouring ramets in better environments. Benefits to supported ramets may be costs to the supporting ramets (Pitelka and Ashmun, 1985; Salzman and Parker, 1985; de Kroon and Schieving, 1990; Caraco and Kelly, 1991). A fitness benefit results if these various costs and benefits to ramets lead to a net benefit at the level of the genet (de Kroon and Schieving, 1990; Eriksson and Jerling, 1990; Caraco and Kelly, 1991).

A clear distinction between supported and supporting ramets, however, may be absent when neighbouring patches have complementary attributes, such as high light and low moisture bordering high moisture and low light (Stuefer *et al.*, 1996). In such cases, benefits of physiological integration may potentially accrue to ramets in both types of environment. In addition, in many circumstances, the spatial pattern of environmental variation changes with time (Washitani and Tang, 1991; Afzal and Adams, 1992; Groffman *et al.*, 1993; Ryel *et al.*, 1996; Alvarez-Rogel *et al.*, 1997); in such cases, different patches may complement one another by being favourable at different times. All of these scenarios potentially lead to net benefits at the genet level due to buffering of variation in space by physiological integration.

When we speak of physiological integration as buffering spatial variation, we really mean that the net effect of poor conditions is reduced, or, in the case of complementary environments, the net effects of local specific deficiencies are reduced. In contrast, some authors have examined the reduction in the spatial variance in growth due to physiological integration (Hartnett and Bazzaz, 1985). Although reduction in variance is a valid meaning of 'buffering spatial variation', it is not what we mean here, because there is no reason for reduction in spatial variation alone to have a fitness benefit to the genet. Here, we refer specifically to a biased situation in which poor conditions or deficiencies are diminished without equivalent costs, so that there is a net fitness benefit at the level of the genet.

An appropriate quantitative framework is needed to assess whether physiological integration does indeed lead to this hypothesized net benefit in a variable environment. Steady development of experimental approaches and corresponding quantitative methods can be

seen in the literature on physiological integration (Noble and Marshall, 1983; Salzman and Parker, 1985; Abrahamson *et al.*, 1991; Stuefer *et al.*, 1994). Here we build on this previous work, suggest some improvements and place measures of the benefits of physiological integration within a defined framework of plant growth models. The results are measures of the overall net fitness benefit of physiological integration, measures for dissecting out various aspects of physiological integration, theoretical predictions about the circumstances under which physiological integration could have fitness benefits, and recommendations on the conduct and interpretation of physiological integration experiments. These results show that there are many subtleties in the study of physiological integration, implying a need for special care in the analysis of physiological integration experiments if valid conclusions about fitness benefits are to be made. These methods are being applied elsewhere (Peterson and Chesson, in press) to understand the benefits of physiological integration in the stoloniferous herb, *Hydrocotyle peduncularis* (R. Brown ex A. Richards). Key notation is provided in Table 1.

FITNESS IN CLONAL PLANTS

Most experiments on physiological integration use biomass at the end of an experiment to assess treatment effects. However, final biomass values are highly dependent on details of an experiment, such as initial biomass and duration, which are often incidental to the questions being asked. To obtain more fundamental measurements in general studies of plant growth, plant physiologists commonly correct final biomass for initial biomass

Table 1. Key notation

a_{Pc}, a_{Oc}, a_{P-+}, a_{P--}, etc.	Allocation, respectively, to parent and offspring sections in environment c, and parent sections in environments −+ and −−, etc.
c	Environmental conditions experienced by a genet fragment: ++, −−, +− or −+; for example, c = +− means a good environment for the parent section and a poor environment for the offspring section
$NetBen$	Short-term net benefit of physiological integration
$NetBen_{-+}$, $NetBen_{+-}$	Short-term net benefit from −+ and +− configurations, respectively
O_{++}, O_{--}, O_{+-}, O_{-+}	Offspring component relative growth rates for the four environments – see c above
p	Fraction of −+ environments among all −+ and +− environments
P_{++}, P_{--}, P_{+-}, P_{-+}	Parent component relative growth rates for the four environments – see c above
q	$1 - p$
R_c, R_{++}, R_{--}, R_{+-}, R_{-+}	Genet fragment relative growth rates in environments c, ++, −−, +−, −+, respectively
R_{P-+}, R_{P--}, R_{O-+}, R_{O--}, etc.	Relative growth rates of parent and offspring sections in environments −+ and −−, etc.
t	Time, duration of an experiment, or period of assessment of physiological integration
W	Biomass of a genet fragment

and time to obtain the *relative growth rate* (Evans, 1972). The relative growth rate is a fundamental quantity in the sense that it can perform predictive, characterization and diagnostic functions. For example, under the null model of exponential growth, the relative growth rate predicts final biomass for times and initial biomasses not studied, and it can be used as a parameter in broader investigations. If growth is not exponential, the dependence of the relative growth rate on time and initial biomass characterizes the deviation from the null model, potentially with important information about biological processes. We argue here that relative growth rate, measured at the level of the whole genet, can perform these fundamental roles in physiological integration studies, and is an important component of fitness, as previously emphasized by Stoner (1989) for the study of clonal Ascidians.

The relative growth rate is normally defined instantaneously in time as

$$\frac{1}{W}\cdot\frac{\mathrm{d}W}{\mathrm{d}t} \tag{1}$$

where W is the biomass. Measurements over finite (not instantaneous) intervals of time use the formula

$$\frac{\ln W(t) - \ln W(0)}{t} \tag{2}$$

(i.e. simply the difference between the natural log final and initial biomasses divided by time). When growth is exponential, this quantity is independent of both time and initial mass and, therefore, corrects the data for uncontrolled variation in these factors. If growth is not exponential, such correction is imperfect and both time and initial biomasses should be controlled or accounted for in analyses and conclusions. However, the relative growth rate remains a useful quantity.

Fitness is commonly regarded as the rate at which zygotes produce new zygotes (Harper, 1985) and is frequently quantified using r, the instantaneous per capita rate of increase (Stearns, 1992). In clonal plants, fitness is a function of both genet and ramet dynamics (Sackville Hamilton *et al.*, 1987): genet dynamics because of sexual reproduction (Harper, 1981; Pitelka and Ashmun, 1985; Eriksson and Jerling, 1990) and ramet dynamics because these modules are the source of totipotent meristems from which the genome is replicated, both vegetatively and sexually (Buss, 1985; Caswell, 1985; Sibly, 1989; Fagerström, 1992; Wikberg, 1995).

Pedersen and Tuomi (1995) emphasized that natural selection may act on the hierarchical levels of both the genet and the ramet, but in many clonal plant systems it is impractical to measure fitness in terms of genet dynamics because of the relative rareness of seedling recruitment (Eriksson, 1989; Nault and Gagnon, 1993; Shimizu *et al.*, 1998) and the potential for genets to be extraordinarily long-lived (Cook, 1985). Importantly, rareness of seedling recruitment relative to ramet recruitment argues that the rate of production of new ramets may dominate genet fitness. Moreover, when the number of ramets is a good predictor of seed production, a ramet-based measure of fitness is sufficient. Such ramet-based measures of fitness have been used in models of evolutionary demography (Caswell, 1985; Nault and Gagnon, 1993; Silvertown *et al.*, 1993; Carlsson and Callaghan, 1994; Okland, 1995; Pedersen, 1995; Wikberg, 1995; Erschbamer *et al.*, 1998; Shimizu *et al.*, 1998). However, such measures might be improved by taking account of ramet size. Size is

positively correlated with survival, ramet production and sexual reproductive capacity in clonal plants (Newell *et al.*, 1981; Hutchings, 1983; Goldberg, 1988; Nault and Gagnon, 1993; Okland, 1995; Worley and Harder, 1996; Cain and Damman, 1997; Hara and Herben, 1997; Laterra *et al.*, 1997; Wijesinghe and Whigham, 1997; Mendoza and Franco, 1998; Piqueras and Klimes, 1998). Modifying a ramet-based r to take account of ramet size gives the relative growth rate of the genet, as defined above. The methods developed below, however, apply equally well to the ramet-based fitness measure r, and would apply also to a complete measure of r that included seedling recruitment as well as ramet recruitment. However, for a more focused development addressing the sort of experiments and data often used in the assessment of physiological integration, we restrict attention for the most part to the relative growth rate component of fitness. Useful variations on the relative growth rate, however, are discussed in the section below on 'Equilibrium scenarios'.

As the genet is the genetic individual, it is the relative growth rate of the entire genet that should be estimated in experimental studies of fitness. In general, this requirement will mean combining biomasses over fragmented parts of a genet distributed over a spatially heterogeneous environment. Such considerations naturally lead to questions of how different parts of a genet, experiencing different conditions, contribute to genet growth, and how physiological connections between parts of a genet may affect such contributions.

QUANTIFYING THE EFFECTS OF PHYSIOLOGICAL INTEGRATION

A genet becomes fragmented by the decay or severing of stolons or rhizomes into sets of ramets connected to each other, but not connected to other ramets in the genet. Such fragments have been referred to by a variety of names in the past, of which 'genet unit' (Hartnett and Bazzaz, 1985) and 'clonal fragment' (Abrahamson *et al.*, 1991) are the most notable, but we suggest the term 'genet fragment' as more evocative. Different genet fragments are not connected and so there can be no physiological integration between them. However, there can be physiological integration between ramets within a fragment or, more generally, between collections of ramets or 'sections' of the same fragment.

A common experimental design in the literature, which we shall refer to as the 'paired-section design', assesses the effects of physiological integration between sections experiencing contrasting environmental conditions (Salzman and Parker, 1985; Stuefer and Hutchings, 1994; Stuefer *et al.*, 1994). Each experimental unit is a genet fragment consisting of two sections connected across the boundary between two distinct environmental patches. Normally, one section in each of these genet fragments gave rise to the other through clonal growth, and so the sections can be labelled as 'parent' and 'offspring'. The patches are of two contrasting types, which we label as '+' and '−' following convention (Stuefer *et al.*, 1994), and are often thought of as good and bad, but need not be strictly good and bad, just environmental contrasts. There are four possible treatment combinations for a genet fragment (++, +−, −+ and −−), where the first sign refers to the environment of the parent patch and the second the environment of the offspring patch. Plants growing in natural environments will be subject to more complex environmental combinations than those considered in this experimental design. Fortunately, both this design and the methods discussed here can be generalized, as indicated in the Discussion section, although this design remains a natural starting point for the investigation of physiological integration in heterogeneous environments.

In the paired-section experiment, the treatments can be grouped as the pairs (+−, −+) and (++, −−) representing contrasting arrangements of genet fragments over a heterogeneous landscape. Under (+−, −+), 'heterogeneous conditions', physiological integration between environments may occur. Under (++, −−), 'homogeneous conditions', both sections of the genet fragment are in the same environment, and so no physiological integration between contrasting environments is possible. Heterogeneous and homogeneous conditions both expose sections collectively to the same array of environmental conditions. Only physiological integration between contrasting environments can lead to a difference between the heterogeneous and homogeneous groups in the combined growth of all sections within these grouped treatments. Thus, comparing the performances of heterogeneous and homogeneous groupings allows the benefits of physiological integration to be assessed. It is this feature that is important to preserve when the design is generalized for more complex scenarios.

In the paired-section design, let R_c be the relative growth rate of a genet fragment growing under some particular conditions, c, where c is one of +−, −+, ++ and −−. The mass of one of these genet fragments at some time t, in terms of its mass at a given time zero, is

$$W_c(t) = W_c(0)\mathrm{e}^{R_c t} \tag{3}$$

Note that if the relative growth rate, R_c, of the genet fragment is constant over the period of time in question, equation (3) implies exponential growth. However, this assumption is not important for all of our development, and only becomes an issue when we discuss the time-dependence of physiological integration below. Otherwise R_c can simply be thought of as the observed relative growth rate, as defined by formula (2), for the period of time 0 to t, with W_c replacing W in (2) and no exponential growth assumption being necessary.

The total mass of the genet at time t is the sum over all genet fragments,

$$\sum_c W_c(t) = \sum_c W_c(0)\mathrm{e}^{R_c t} \tag{4}$$

Therefore, the average relative growth rate of the genet over the interval of time zero to t is

$$\frac{\ln\{\sum_c W_c(t)\} - \ln\{\sum_c W_c(0)\}}{t} = \frac{1}{t}\ln\left\{\frac{\sum_c W_c(0)\mathrm{e}^{R_c t}}{\sum_c W_c(0)}\right\} \tag{5}$$

which is just the change in total ln genet biomass for the period divided by the amount of time elapsed. This expression simplifies substantially when initial fragment masses are all the same, as might be arranged in experimental circumstances. Then, genet relative growth rate becomes

$$\frac{1}{t}\ln\left\{\frac{1}{n}\sum_c \mathrm{e}^{R_c t}\right\} \tag{6}$$

where n is the number of different conditions c experienced by fragments of that genet. By evaluating this formula for the heterogeneous treatments, +− and −+, we obtain the relative growth rate of a genet whose fragments all span the boundary of the two contrasting environments, with parent and offspring sections equally represented in the two types of environment. Subtracting off the relative growth rate for homogeneous conditions (−− and ++) gives the following expression for the net benefit of physiological integration over an environmental boundary:

$$\frac{1}{t}\ln\left\{\frac{1}{2}(e^{R_{-+}t}+e^{R_{+-}t})\right\}-\frac{1}{t}\ln\left\{\frac{1}{2}(e^{R_{--}t}+e^{R_{++}t})\right\} \quad (7)$$

This expression is a general one and does not require growth to be exponential, provided the relative growth rates are measured by expression (2) with the same t as used in expression (7). However, unless growth is exponential, or another specific model of growth is provided, no predictions are possible for other periods of time. As we shall see below, however, net benefits of physiological integration may vary with time even when growth is exponential.

First, we consider the net benefit of physiological integration over very short periods of time, which also provides us with a simpler measure of the net benefit of physiological integration and one of great utility. To obtain this measure, we take the mathematical limit of (7) as the interval of time becomes small to obtain:

$$NetBen=\frac{R_{-+}+R_{+-}}{2}-\frac{R_{--}+R_{++}}{2} \quad (8)$$

This expression is designated *NetBen* because it can be rightly thought of as the net benefit of physiological integration in the short term. It will be valid for all intervals of time that are short enough, as discussed below. The quantity *NetBen* has a very simple and intuitive interpretation: There is a net benefit of physiological integration between heterogeneous conditions if the average relative growth rate of genet fragments growing under heterogeneous conditions exceeds the average relative growth rate of genet fragments growing under homogeneous conditions. This measure is related to the 'homogeneous versus heterogeneous test' of Stuefer *et al.* (1994), which, however, is based on uncorrected final biomass rather than the relative growth rate.

TIME DEPENDENCE OF NET BENEFITS OF PHYSIOLOGICAL INTEGRATION

The derivation of *NetBen* above for exponentially growing genet fragments depends on the assumption that the relevant time period is short. Just what does 'short' mean, and what errors might occur if the time period is not short? Jensen's inequality from probability theory (Needham, 1993) shows that expression (6) for the genet relative growth rate satisfies the inequality

$$\frac{1}{t}\ln\left\{\frac{1}{n}\sum\nolimits_c e^{R_c t}\right\}>\frac{1}{n}\sum\nolimits_c R_c \quad (9)$$

Thus, the relative growth rate of the genet is in fact greater than the average of the relative growth rates of its constituent fragments. This result remains true for the more general case (expression 5) involving weighted averages. This sort of phenomenon is a critical issue in the literature on population growth in a variable environment, where it is referred to as 'nonlinear averaging' (Chesson, 1996). Assuming constant values of R_c (exponential growth), this inequality grows with time in a way that depends on the variance of the individual fragment relative growth rates. Taking the mathematical limit, it is seen that the left-hand side of inequality (9) converges on the maximum value of R_c. Thus, the actual relative growth rate experienced by a genet is biased upwards towards the growth rates experienced by faster growing fragments.

These considerations mean that the validity of *NetBen* as a measure of the benefits of physiological integration is affected by the time interval involved when the growth rates of genet fragments are constant. In this case, Taylor expansion shows that the difference between the finite-time net benefit of physiological integration (7) and *NetBen* is approximately equal to

$$\frac{1}{2}\left[\left(\frac{R_{-+}-R_{+-}}{2}\right)^2-\left(\frac{R_{--}-R_{++}}{2}\right)^2\right]t \tag{10}$$

[i.e. the finite-time value (7) exceeds *NetBen* by approximately this amount]. The term inside square brackets in expression (10) is equal to the difference between the variance of the relative growth rates for genet fragments growing under heterogeneous conditions and the variance of the relative growth rates for fragments growing under homogeneous conditions. Note that this deviation from *NetBen* also grows linearly with time. Expression (10) can be used as a correction to *NetBen* for small values of t and also as an indication of how the benefits of physiological integration change with the time interval involved.

In the case where – and + refer simply to unfavourable and favourable environments, it is likely that $R_{+-} - R_{-+}$ is smaller in magnitude than $R_{++} - R_{--}$. In this case, expression (10) shows that the net benefit of physiological integration must decrease with time and, therefore, *NetBen* measures the maximum benefit of physiological integration. Whenever expression (10) is large, however, expression (7) should be used to give an accurate value for the specific net benefit for the particular time interval of interest.

Constant growth rates of genet fragments mean that, ultimately, the difference in genet growth rates for heterogeneous versus homogeneous conditions approaches

$$\max(R_{-+}, R_{+-}) - \max(R_{--}, R_{++}) \tag{11}$$

[let time go to infinity in expression (7)]. Thus, in the long run, the net benefit of physiological integration is simply the maximum relative growth rate for fragments growing in heterogeneous conditions minus the maximum relative growth rate for fragments growing in homogeneous conditions. Thus, in the long run with constant growth rates, there is only a positive net long-term benefit of physiological integration over a heterogeneous environment when growth under at least one of the heterogeneous conditions is superior to growth under either homogeneous condition.

If the environments are strictly favourable and unfavourable, as suggested by our notation, then a positive long-term benefit is unlikely, since presumably growth under ++ exceeds growth under all other conditions. On the other hand, the contrast between + and – may simply distinguish different environments rather than rank them in all respects – for example, the environments may be complementary, as discussed above, in which a 'division of labour' between sections in different environments might take place (Stuefer *et al.*, 1996). In such cases, each heterogeneous condition may have distinct advantages over each homogeneous condition, meaning that expression (11) would be positive, and there would be a net benefit of physiological integration on any time-scale.

COSTS AND BENEFITS WITHIN A GENET FRAGMENT

Insight on the mechanisms leading to net benefit of physiological integration may be obtained by decomposing *NetBen* into specific measures of costs and benefits at the section

level. In an important advance, Salzman and Parker (1985) and Stuefer *et al.* (1994) proposed cost and benefit measures by asking about the effect on a section's growth of the environment of a section's partner. However, these authors used unadjusted final biomasses in this assessment, which we argue against above. Hence, we modify their approach to obtain measures that combine to yield *NetBen*.

Ideally, costs and benefits should be measured in common currency on an additive scale so that their differences are in fact the net benefits. To achieve such additivity, we use the technique of component relative growth rates introduced by Hunt and Bazzaz (1980). The component relative growth rate, CRGR, is the ratio of the rate of increase of a particular component of a plant (e.g. a section of a genet fragment) to the mass of the plant as a whole (in this case, the genet fragment). The units are g[section]·g[fragment]$^{-1}$·day^{-1}. The instantaneous CRGR of the ith section of a genet fragment experiencing condition c is simply

$$\frac{1}{W_c}\cdot\frac{\mathrm{d}W_{ci}}{\mathrm{d}t} \tag{12}$$

where W_{ci} = the dry mass of the ith section of the genet fragment. The sum of all sectional CRGRs of a genet fragment gives the relative growth rate of the genet fragment (Hunt and Bazzaz, 1980).

For practical measurement, the instantaneous CRGR defined by expression (12) must be replaced by its time average over some period of time, i.e.

$$\frac{1}{t}\int_0^t \frac{1}{W_c}\cdot\frac{\mathrm{d}W_{ci}}{\mathrm{d}t}\,\mathrm{d}t \tag{13}$$

This expression cannot be evaluated in terms of initial and final masses without further information, such as the nature of the relationship between component masses and total mass. As an approximation, one might use a linear relationship between W_c and W_{ci}: $W_{ci} = a + bW_c$, where the constants a and b may depend on both c and i. Then the time average CRGR (expression 13) can be shown to equal

$$\frac{(W_{ci}(t) - W_{ci}(0))(\ln W_c(t) - \ln W_c(0))}{t(W_c(t) - W_c(0))} \tag{14}$$

which involves only final and initial masses and so is readily available experimentally.

Given the CRGRs for the sections of a genet fragment, *NetBen* (expression 8) becomes

$$NetBen = \frac{P_{-+} + O_{-+} + P_{+-} + O_{+-}}{2} - \frac{P_{--} + O_{--} + P_{++} + O_{++}}{2} \tag{15}$$

where P and O refer to the CRGRs of parent and offspring sections, respectively, of a genet fragment experiencing the conditions indicated by the subscripts. Note that $P + O = R$. From these CRGRs, we can now define cost and benefit measures at the sectional level. For parent sections,

$$CostP = P_{++} - P_{+-} \tag{16}$$

which defines the cost, in terms of a changed CRGR, that a parent section in a good patch (an 'unstressed section') experiences due to its connection to a section in a poor patch

(a 'stressed section'). The benefit to a stressed parent section from its connection to an unstressed partner is defined as

$$BenP = P_{-+} - P_{--} \tag{17}$$

with the corresponding definitions, $CostO = O_{++} - O_{-+}$, $BenO = O_{+-} - O_{--}$, for offspring sections. Combining these various costs and benefits leads back to *NetBen*:

$$NetBen = \tfrac{1}{2}BenP + \tfrac{1}{2}BenO - \tfrac{1}{2}CostP - \tfrac{1}{2}CostO \tag{18}$$

and thus we see that costs and benefits are defined in such a way that a net benefit occurs at the level of the genet simply if total sectional benefits exceed total sectional costs.

Further important information is obtained by expressing these cost and benefit measures in terms of sectional relative growth rates, as opposed to sectional CRGRs, and relative allocations of mass to sections. This can be done with all cost and benefit measures, but we illustrate it here just for *BenP*. For simplicity, we deal only with the instantaneous time-scale. Let a_{P-+} and a_{P--} be the ratios of the parent section masses to the total genet fragment mass, respectively, for the −+ and −− treatments, and let R_{P-+} and R_{P--} be the actual relative growth rates of the sections. Note that the CRGRs are simply the products of the *a*s and *R*s (e.g. $P_{-+} = a_{P-+}R_{P-+}$). To focus on the effects of changes in allocation versus the effects of changes in relative growth rate, we define $\Delta a = a_{P-+} - a_{P--}$ and $\Delta R = R_{P-+} - R_{P--}$ and then, after a little algebra, *BenP* can be rewritten as

$$BenP = \Delta R \cdot a_{P--} + \Delta a \cdot R_{P--} + \Delta R \cdot \Delta a \tag{19}$$

Thus, *BenP* is equal to the difference of sectional relative growth rates, weighted by a_{P--}, plus the difference in allocation, Δa, weighted by R_{P--}, plus their interaction ($\Delta R \cdot \Delta a$).

Support of a parent section in a poor environment by an offspring section in a good environment should most clearly be reflected by a positive value of ΔR – that is, higher relative growth of a supported section compared with an unsupported section. This effect may be modified up or down by the sectional allocation. In an experimental setting, sectional allocations may often be part of the design, suggesting non-uniqueness of these cost and benefit measures. However, growth of a genet fragment may be expressed as a matrix model with linear sectional growth rates and material exchange rates. Then, the standard predictions of matrix analysis (Bellman, 1974) imply that, after an initial period of adjustment, sectional allocations settle down to constant values, at which point the entire genet fragment grows exponentially. Thus, provided an experiment includes an adequate initial period of adjustment, matrix growth models imply that sectional allocations are not arbitrary, but instead are determined by the growth and integration of sections. Such matrix models also predict that, after the initial adjustment period, both sections grow at the same exponential rate as the genet fragment as a whole because physiological integration adjusts the growth rates of both sections to the same rate. Thus, for any treatment combination *c*, $R_{Pc} = R_{Oc} = R_c$, in the long run.

SYMMETRY OF INTEGRATION

The CRGRs can be used to determine whether parent and offspring sections contribute equally to the net benefit of physiological integration. *NetBen* can be split into two additive components giving net benefit contributions, respectively, due to parent and offspring sections:

$$NetBen = NetBenP + NetBenO \tag{20}$$

where

$$NetBenP = \frac{P_{-+} + P_{+-}}{2} - \frac{P_{--} + P_{++}}{2} \tag{21}$$

and

$$NetBenO = \frac{O_{-+} + O_{+-}}{2} - \frac{O_{--} + O_{++}}{2} \tag{22}$$

Related to this question of the net benefits from parent and offspring sections is the issue of which arrangement, −+ or +−, of a genet fragment confers the greatest net benefit. This question leads to yet another way of subdividing net benefits: $NetBen_{-+} = R_{-+} - (R_{--} + R_{++})/2$ and $NetBen_{+-} = R_{+-} - (R_{--} + R_{++})/2$, which measure net benefits for specific arrangements. The difference between these,

$$NetBen_{-+} - NetBen_{+-} = R_{-+} - R_{+-} \tag{23}$$

can be used as the basis of a test of equivalence of these arrangements. If one arrangement is appreciably better, then it might be expected to be favoured in nature. In that case, the overall net benefit of physiological integration applicable to a natural system might be recalculated weighting +− and −+ groups unequally, thus reflecting an actual or expected pattern in nature. The appropriate formula for *NetBen* would then be

$$NetBen = pNetBen_{-+} + qNetBen_{+-} \tag{24}$$

where p and q are the relative frequencies of the −+ and +− arrangements. With $p = q = 1/2$, the original definition (8) of *NetBen* is recovered.

This division (24) of *NetBen* into $NetBen_{-+}$ and $NetBen_{+-}$ decomposes the genet level in terms of the genet-fragment level. To complete a decompositional hierarchy, the genet-fragment level net benefits can be related to section-level net benefits with symmetry adjustments for the arrangement of the genet fragment. For example, $NetBen_{-+} = NetBenP - (P_{+-} - P_{-+})/2 + NetBenO + (O_{-+} - O_{+-})/2$. In effect, due to the particular arrangement of the genet fragment, *NetBenP* is adjusted down by half the difference between a supporting and a supported parent section, and *NetBenO* is adjusted up by the opposite quantity for offspring sections.

THE NULL HYPOTHESIS OF NO PHYSIOLOGICAL INTEGRATION

The detailed analysis of physiological integration provided above depends on the assumption that genet fragments have constant relative growth rates. There are two important ways in which such constant growth might arise in an experiment. First, measurements might be taken over short periods that do not allow enough time for appreciable change in relative growth rate. Second, the first and final measurements might span a longer time provided the first measurement is after an initial period of adjustment to the experimental conditions and the final measurement is before crowding or senescence has set in. This prediction follows from a matrix formulation of genet growth as discussed above. Moreover, sections grow at the same exponential rate as the genet fragment as a whole. However, if there is

no physiological integration, exchange of materials makes no contribution, and sections growing in poorer environments maintain lower relative growth rates. We now use this fact to develop a test for the presence of physiological integration, as distinct from the dominant question addressed above – that is, the net benefit of physiological integration.

Without physiological integration, the relative growth rate of a genet fragment growing for a period of time t under conditions c would be

$$R_c = \frac{1}{t}\ln\left(a_{Pc}e^{R_{Pc}t} + a_{Oc}e^{R_{Oc}t}\right) \tag{25}$$

where a_{Pc} and a_{Oc} are the initial allocations to parent and offspring sections, respectively (in terms of the ratio of section mass to genet fragment mass, as defined earlier), and R_{Pc} and R_{Oc} are the corresponding sectional relative growth rates, which we assume to be constant. For small t, this relative growth rate converges on the weighted average, $a_{Pc}R_{Pc} + a_{Oc}R_{Oc}$, of the sectional relative growth rates. Substituting this in the formula (8) for *NetBen*, assuming equal allocation to sections, leads to

$$NetBen = \frac{R_{P-+} + R_{O-+} + R_{P+-} + R_{O+-}}{4} - \frac{R_{P--} + R_{O--} + R_{P++} + R_{O++}}{4} \tag{26}$$

which rearranges to

$$NetBen = \frac{(R_{P-+} - R_{P--}) + (R_{O+-} - R_{O--})}{4} - \frac{(R_{P++} - R_{P+-}) + (R_{O++} - R_{O-+})}{4} \tag{27}$$

Here, *NetBen* neatly divides into section-level costs and benefits in terms of relative growth rates of genet fragments – for example, $BenP = (R_{P-+} - R_{P--})/2$. With no physiological integration, these costs and benefits are all zero (the relative growth rate of a section does not depend on the environment of its partner), and expression (26) for *NetBen* is, of course, equal to zero because there is no physiological integration. A non-zero value of *NetBen*, as defined by expression (27), means that physiological integration is occurring and, indeed, it would indicate also an overall net benefit or net cost depending on whether it is positive or negative. Examination of the individual terms would give more information on the pattern of integration. Examination of expression (27) reveals that, for this test to be useful, it is not necessary for the sectional relative growth rates to be measured over a short period of time, or for sectional relative growth rates themselves to be constant over time, because in the absence of physiological integration each of the terms in parentheses in (27) would be zero regardless of these other details.

Expression (27) assumes that the initial sectional allocations are equal. This may not always be desirable, and a useful extension of the formula above is to the case where the sectional allocation depends both on the environment in which it is present and its status as parent or offspring. Note that, under the null hypothesis of no physiological integration, the environment of the partner should not have a role, and so the allocation for P_{--}, for instance, is given as a_{P-}, with no third subscript. These allocations would be estimated in an experiment averaging over the partner environment. Then, expression (27) generalizes to

$$NetBen = \frac{a_{P-}(R_{P-+} - R_{P--}) + a_{O-}(R_{O+-} - R_{O--})}{2} - \frac{a_{P+}(R_{P++} - R_{P+-}) + a_{O+}(R_{O++} - R_{O-+})}{2} \tag{28}$$

which can form the basis for testing for physiological integration in this more general setting. Note, however, that if physiological integration occurs, the sectional allocations would depend on the partner environment, and the actual net benefit of physiological integration would then have to be quantified by the original expression (8) for *NetBen*.

The tests above are especially important when the relative growth rates of genet fragments are estimated over a finite interval of time of length t to avoid falsely concluding that there is net benefit to physiological integration by blind application of formula (8) for *NetBen*. Without first testing for physiological integration, or having some reason to expect that the growth of genet fragments is constant for the relevant period of time, formula (8) could lead to the false conclusion of a net benefit of physiological integration if time t is too large. This problem is most readily understood for the special case where the sectional relative growth rate is independent of whether it is parent or offspring, and also independent of the environment of its partner. Designating R_+ and R_- as the sectional relative growth rates for + and – environments, respectively, *NetBen* estimated by expression (8) yields

$$\frac{1}{t}\ln\left\{\frac{1}{2}(e^{R_- t}+e^{R_+ t})\right\}-\left\{\frac{1}{2}(R_-+R_+)\right\} \tag{29}$$

Unless there is also no effect of environment on growth ($R_+ = R_-$), Jensen's inequality shows that this expression is always positive, because of non-linear averaging. Thus, a false impression of a net benefit of physiological integration would result when, in fact, there is no physiological integration. Similar errors can be seen in the sectional cost and benefit measures. With strictly good and bad environments, the Δa term of equation (19) for *BenP* would be negative and ΔR would be zero, leading to a negative benefit, when in fact there would be no effect. This absence of an effect, however, would be indicated by the zero value of ΔR, emphasizing value in expressing sectional cost and benefits in terms of differences in sectional relative growth rates and sectional allocations.

The presence of these seemingly strange effects in the absence of physiological integration is due to the fact that genet fragments should not have constant relative growth rates when their sections have different temporally constant relative growth rates. For example, expression (25) above shows that the relative growth rate of the genet fragment increases with time from the weighted average of the sectional relative growth rates, $a_{Pc}R_{Pc} + a_{Oc}R_{Oc}$, to the greater of their two values, $\max[R_{Pc}, R_{Oc}]$, when there is no physiological integration between sections.

EQUILIBRIUM SCENARIOS

Exponential growth of genet fragments, or sections of genet fragments, might imply unlimited space in which to expand, at least over the periods of time under consideration. At the opposite extreme, there is no room to expand because the vegetation has achieved steady-state cover within a defined area. This scenario, however, does not mean that there is no fitness to assess because the vegetation may have excess production over that needed to maintain a steady state. This excess may be exported, for example, as seed, to unfilled habitat. The magnitude of excess production relative to the size of the genet is essentially a relative growth rate, and may be thought of as a measure of fitness provided the size of the genet itself is determined by the habitat within which it is confined, not the genet's geno-

type. As the size of the genet does not change over time, net benefits of physiological integration based on this relative growth rate will only vary through time to the extent that differences between relative growth rates, determined instantaneously, are time-dependent. A key issue here, however, is determining the size of a genet. If genets confined to poor patches achieve a low biomass at steady state, and have proportionately low total production, a relative growth rate defined in terms of biomass may not reflect low production in poor patches. However, if size is defined in terms of area occupied, production per unit size (i.e. per unit area) will reflect those poor conditions. To make this a proper relative growth rate, production should be measured as area per unit time – for example, new area colonized by production from the genet. However, expressing production in area terms is not essential for our development here and would often be cumbersome and artificial even though an area measure of production might be possible in most circumstances.

Exported production might be defined and measured in a variety of different ways. Seed production, as mentioned above, is conceptually simplest, although not always the most convenient. Other measures might involve sponsorship of growth of the genet itself beyond a defined area that it has filled. There are a variety of ways such sponsorship might be defined and measured, but in practice imperfect measures are likely to be used, such as the weight of shoots clipped off as they pass out of the defined area in a unit of time.

Having defined an appropriate relative growth rate measure for a genet fragment in this steady-state context, the measure *NetBen* defined above by equation (8) can be used, as can the various decompositions of it at the fragment and section levels. All discussions of time dependence above are inapplicable, however, because in this steady-state scenario the relative sizes of genet fragments, and the relative sizes of sections, do not change with time. Thus, time dependence of the genet relative growth rate can only arise if genet fragment relative growth rates are time-dependent, and these can only be time-dependent if sectional relative growth rates are time-dependent. Thus, physiological processes would have to respond to time on the smallest spatial scale, and time dependence of the genet relative growth rate would reflect this small-scale time dependence only.

APPLYING THIS FRAMEWORK TO DATA ANALYSIS

The formulae given here apply directly to the paired-section experiment where a genet fragment represents an independent experimental unit and the ++, +−, −+ and −− are the treatments in a 2×2 factorial, with the environment of the parent section being one factor and the environment of the offspring section being the other factor. Within this design, many of the quantities specified here are estimated as linear contrasts (Neter *et al.*, 1996). For example, for the key quantity *NetBen*, the basic data are the relative growth rates for each genet fragment in the experiment; the means of these relative growth rates within treatments estimate the quantities R_{-+}, R_{+-}, R_{--} and R_{++}, and *NetBen* is the linear contrast in these means defined by expression (8) (see Table 2). A confidence interval for *NetBen* can be obtained using standard methods for linear contrasts.

Table 2 lists the key quantities that might form the focus of physiological integration experiments, and they are given in the order in which they might be applied to the data. First, one should check for the presence of physiological integration with expression (27). In cases where exponential growth is reasonable, physiological integration would be indicated if any of the quantities in parentheses in expression (27) were significantly non-zero. As these are not independent, a multivariate approach would be appropriate, or a cruder

Table 2. Application of formulae to data analysis

Formula	Number	Application
$\frac{1}{4}(R_{P-+} - R_{P--}) + \frac{1}{4}(R_{O+-} - R_{O--}) - \frac{1}{4}(R_{P++} - R_{P+-}) - \frac{1}{4}(R_{O++} - R_{O-+})$	(27)	Testing for the presence of integration
$NetBen = \frac{R_{-+} + R_{+-}}{2} - \frac{R_{--} + R_{++}}{2}$	(8)	Measuring short-term net benefit of integration
$\frac{1}{2}\left[\left(\frac{R_{-+} - R_{+-}}{2}\right)^2 - \left(\frac{R_{--} - R_{++}}{2}\right)^2\right]t$	(10)	Assessing time dependence of net benefits
$\frac{1}{t}\ln\left\{\frac{1}{2}(e^{R_{-+}t} + e^{R_{+-}t})\right\} - \frac{1}{t}\ln\left\{\frac{1}{2}(e^{R_{--}t} + e^{R_{++}t})\right\}$	(7)	Average net benefit for a fixed period of time
$NetBenP = \frac{P_{-+} + P_{+-}}{2} - \frac{P_{--} + P_{++}}{2}$	(21)	Net benefit due to parent sections
$NetBenO = \frac{O_{-+} + O_{+-}}{2} - \frac{O_{--} + O_{++}}{2}$	(22)	Net benefit due to offspring sections
$NetBen_{-+} - NetBen_{+-}$	(23)	Symmetry of integration
$NetBen = pNetBen_{-+} + qNetBen_{+-}$	(24)	Short-term net benefits with unequal frequencies of −+ and +− arrangements

Bonferroni adjustment for multiple comparisons could be used. However, the contrast as a whole is suitable for testing whether there is integration in the direction of an overall net benefit or net cost. Testing this hypothesis is simpler, and likely to have higher power when physiological integration has important effects. To apply linear contrast methods to expression (27), it is best to rearrange it so that it takes the form $\frac{1}{4}(R_{P-+} + R_{O-+}) + \frac{1}{4}(R_{O+-} + R_{P+-}) - \frac{1}{4}(R_{P++} + R_{O++}) - \frac{1}{4}(R_{P--} + R_{O--})$, where each of the parenthetical terms contains quantities from the same treatment – that is, parent and offspring relative growth rates for that treatment. Each of these quantities can be estimated for an individual genet fragment, and expression (27) can then be estimated as a linear contrast in the treatment means of the sums of the parent and offspring relative growth rates. This contrast can be tested for deviation from zero by standard univariate linear contrast methods (Neter *et al.*, 1996). If this test yields a significant result, the actual net benefits of physiological integration are then best estimated by *NetBen* as described above.

Time dependence of physiological integration would be examined next using the quantity (10) and, if this were significant, and importantly large for times t of biological interest, expression (7) would be used to estimate actual net benefits for a finite time interval of interest. Information on the mode and mechanism of physiological integration could then be investigated further through the component measures *NetBenP* and *NetBenO*, and the symmetry measure $NetBen_{-+} - NetBen_{+-}$. Except for the tests of time dependence and the presence of physiological integration, all these methods apply also to equilibrium scenarios. In the equilibrium case, it is not necessary to test for the presence of physiological

integration before testing for net benefits because, in the equilibrium case, the test for net benefits is also a valid test for the presence of physiological integration.

DISCUSSION

We have established a quantitative framework for the assessment of the fitness benefits of physiological integration in a heterogeneous environment. It is based on simple models of plant growth that are easily related to experiments. We have shown that, even in the simplest circumstances, there are many subtleties, as discussed below (see 'Theoretical implications'). The presence of these subtleties justifies our exploration of models because it demonstrates that careful quantitative analysis is needed for the assessment of the benefits of physiological integration. Caraco and Kelly (1991) also developed models of physiological integration in clonal plants, but with a very different purpose. They focused on optimization of resource translocation with non-linear growth responses to spatially and temporally varying resources. Our focus is on assessing patterns of benefit from experiments. Although our study has led to theoretical predictions, they are to do with net benefits at the genet level, given patterns of relative growth rates in relation to the environment. Instead, Caraco and Kelly (1991) addressed the physiological mechanisms behind such patterns.

Quantitative methods

Our models and methods focus on the paired-section experiment for ease of exposition, and because it is a common design. However, our methods do generalize, as discussed below. We have argued that, in many circumstances, the genet relative growth rate should be the major component of fitness and also a good indicator of fitness. The paired-section experiment can then be used to address the question, 'Does physiological integration across a heterogeneous environment lead to higher fitness?' Previous approaches to this question have not used relative growth rate, but instead have used final biomasses or log final biomass in paired-section (Salzman and Parker, 1985) or similar experimental designs (Ong and Marshall, 1979; Slade and Hutchings, 1987; Evans, 1988; Price and Hutchings, 1992; Stuefer *et al.*, 1994; Dong, 1995). With appropriate caution – for example, with equal or randomly assigned initial biomasses – the appropriate fitness comparisons are still possible from analysis of final biomasses. However, without adjusting for initial biomass and time, such analyses do not allow comparison of results from different experiments or different systems and are likely to have lower precision. Moreover, the theoretical results given here suggest that the net benefits of physiological integration depend on time, while measures based on final biomasses alone assess benefit for one time only, the duration of the experiment. Interpretation of paired-section and similarly designed physiological integration studies, and a full appreciation of the methods presented here, require understanding of the theoretical findings of this article, as discussed below.

The paired-section design is clearly an extreme simplification of the environmental complexity likely to be found under field conditions. While the paired-section experiment is likely to remain the first step in many physiological integration analyses, the analyses presented here for the paired-section experiment do generalize to more complex situations. For instance, there is no reason to restrict analysis to just two sections in two contrasting environments or to equal initial masses of genet fragments in different environments. The

principle employed here is that the net benefit of physiological integration should be a comparison of the overall relative growth rate for genet fragments growing under heterogeneous conditions with the overall relative growth rate for genet fragments growing under homogeneous conditions. This principle leads to extensions of our methods to as many environmental types and sections of genet fragments as one wishes to contemplate. Extensions of the methods above are straightforward and can be developed easily for any application following the examples given here for the paired-section case. Further extensions might consider not simply the comparison of heterogeneous versus homogeneous conditions, but also the comparison of more complex versus less complex heterogeneity. Rather than explicitly develop methods that cover all these cases, which would necessarily involve complex and rather abstract formulae, we instead use the paired-section design as a generalizable illustration to show how appropriate quantitative methods for physiological integration experiments can be found.

The paired-section design might also be modified to include multiple harvests, which would allow application of these methods beyond the two contrasting growth scenarios, exponential and equilibrium, that were considered here in detail. Although the basic expression (7) gives the net benefit of physiological integration for general growth scenarios, a detailed decomposition of this quantity in terms of fragment and sectional costs and benefits is not available, and in any case would be specific to the time interval on which the measurements were made. A model for change in the relative growth rate over time is needed. This might be found empirically by means of multiple harvests. With a model fitted to such data, the instantaneous net benefit of physiological integration for any time could be calculated using the relative growth rates given by the model. However, in general, the formula (8) for *NetBen* would have to be modified by the relative masses of the genet fragments at a particular time to give $NetBen(t) = f_{-+}(t)R_{-+}(t) + f_{+-}(t)R_{+-}(t) - f_{--}(t)R_{--}(t) - f_{++}(t)R_{++}(t)$, where, for example, $f_{-+}(t) = W_{-+}(t)/(W_{-+}(t) + W_{+-}(t))$. The net benefit over any defined period of time would then be found by simply averaging $NetBen(t)$ over that period of time. In this way, the detailed effects of any growth scenario can be dissected. This dissection may be complex, as our formula for $NetBen(t)$ suggests. Moreover, fragment-level and section-level decompositions that follow from this formulation are nowhere near as straightforward as those arising from the time-independent *NetBen* discussed above. However, such complexity is a reality, and these methods provide a route to understanding that has been lacking in the literature.

Theoretical findings

Our models show that the relative growth rate of a genet consisting of independently growing genet fragments is not likely to have a constant relative growth rate even when those of the constituent genet fragments do not change with time. This means that growth at the genet level is not exponential, even when growth at the level of the genet fragment is exponential. Of most importance, this means also that the net benefit of physiological integration should change with time. In particular, a net benefit observed on a short time-scale might well disappear and become a net cost on a long time-scale. Such changes in net benefit most obviously occur when genet fragments are physiologically integrated between favourable and unfavourable environments, and have relative growth rates less than those found under wholly favourable conditions. In these circumstances, any short-term benefit of physiological integration decreases with time, leading to a net cost.

It is especially important to be aware in experimental studies that the observed benefit or cost of physiological integration might well be specific to the period of time chosen. Exponential growth assumptions are applicable to many experiments in which the investigator prevents crowding and maintains resource levels as the plants grow. The length of an experiment is often chosen on logistical grounds; for example, allowing enough time for large differences between treatments to develop, or allowing enough time for experimental materials to adjust fully to experimental conditions. Such conditions need not reflect important intervals of time for the natural system under study. Thus, unless the time dependence of physiological integration is understood, there is a danger that net benefits or costs will be inferred that to do not correspond to actual net benefits or costs for natural time-scales.

The time dependence found for the net benefit of physiological integration results from differences between the relative growth rates of the genet fragments making up a genet, and the fact that the genet growth rate is not an ordinary (linear) average of the constituent fragment growth rates, except at the initial instant of growth. The genet relative growth rate is instead a non-linear average that becomes more strongly non-linear as time progresses. In biological terms, genet fragments with higher relative growth rates make up progressively more of the genet biomass, and their growth rates come to dominate that of the genet as a whole. The higher the variance between the relative growth rates of the genet fragments making up a genet, the greater the change in the genet growth rate with time because of greater differences between the linear average of the genet fragment growth rates and the maximum of these rates. For example, with + and – representing favourable and unfavourable environments, respectively, large differences are expected between the ++ and −− arrangements of genet fragments, but not necessarily between the −+ and +− arrangements. Thus, there is higher variance between genet fragment relative growth rates under homogeneous conditions (++ and −−) than under heterogeneous conditions (−+ and +−). The relative growth rate of a genet in homogeneous conditions would, therefore, increase with time much more than that of a genet in heterogeneous conditions experiencing physiological integration between environments. Such changes may lead an initial net benefit of physiological integration to become a net cost as time progresses.

This role of variance in the time dependence of physiological integration suggests circumstances in which time dependence may be minimal. If – and + represent complementary environments – for example, each with a specific but different resource deficiency (Stuefer *et al.*, 1996) – then growth under −− need not differ from growth under ++. Heterogeneous conditions (−+ and +−) may then have strictly higher genet-fragment relative growth rates than homogeneous conditions (−− or ++). In these circumstances, there would be a net benefit of physiological integration in both the short term and the long term. Moreover, the net benefit need not be greatly time-dependent, because the variance between genet fragments experiencing homogeneous conditions may be small and similar to variance under heterogeneous conditions.

One case with a similar outcome to such complementary conditions is that of spatio-temporal fluctuations in conditions. Consider the idealized circumstances in which the different patches switch between + and – states. For example, movements on a forest floor can create spatio-temporal fluctuations in light conditions for clonal herbs (Peterson, 1996). A genet fragment experiencing an alternation of −+ and +− on a short time-scale would grow at the long-run rate $(R_{+-} + R_{-+})/2$, whereas a genet fragment experiencing alternately ++ and −− would grow at the long-run rate $(R_{++} + R_{--})/2$. As a consequence, the long-run

net benefit under such alternating environmental conditions would be given by *NetBen* (expression 8), which we previously described as the short-term net benefit of physiological integration. To achieve this value, however, patches must change between + and – states on the time-scale on which our measure of time dependence (expression 10) remains small compared with *NetBen*.

Another reason for a variation on the predictions of time-dependent net benefits of physiological integration is crowding that may occur under natural conditions. In nature, growth under a doubly favourable environment (++) may be restricted by crowding and, in the long run, need not greatly exceed that under heterogeneous conditions, potentially preserving a long-term net benefit of physiological integration. Experimenters often take the trouble to minimize crowding in experiments to increase the chance that relative growth rates will be constant over time, which would also mean exponential growth. The resulting conclusions, however, may not be relevant to long-term growth in the field, where crowding may occur. Several authors have studied important aspects of the effects of crowding on clonal plant growth and mortality (Pitelka, 1984; Briske and Butler, 1989; Carlsson and Callaghan, 1990; Cain *et al.*, 1995; de Kroon and Kalliola, 1995; Pedersen and Tuomi, 1995). To handle cases involving crowding, we assumed an equilibrium scenario where biomass cannot increase within a defined area, and fitness is measured as the export of production from this area. Interestingly, in this case, physiological integration is not predicted to be time-dependent except to the extent that the exported production of a genet fragment is time-dependent, emphasizing the importance of the sorts of details that the methods given here are designed to examine.

In addition to time dependence of net benefits of physiological integration, we found time dependence of the relative growth rates of genet fragments in the case where there is no physiological integration and sections grow at different exponential rates. On a short time-scale, the relative growth rate of a genet fragment is a linear average of its sectional relative growth rates, but for longer periods of time averaging becomes non-linear and the initial linear average is exceeded. This phenomenon can be thought of as a buffering effect of exponential growth in a spatially heterogeneous environment. The long-term relative growth rate is influenced more by growth in favourable patches than in unfavourable patches. Indeed, in the long run, growth in the more favourable patches dominates. Acting on the scale of the genet fragment, this same effect is the cause of time dependence of physiological integration: with time, those genet fragments experiencing the best conditions contribute progressively more to the relative growth rate of the genet fragment as a whole. However, when sections are never physiologically integrated, the buffering effect of exponential growth in a heterogeneous environment alone is present, not any advantage from physiological integration. In this case also, the buffering effect on genet growth is the same for homogeneous conditions (–– and ++) and heterogeneous conditions (–+ and +–) because the array of environments experienced by independently growing sections is the same in these two cases. Without due care, however, the buffering effect of exponential growth could be confused with a benefit of physiological integration. The methods presented here are designed to avoid this possibility.

Further considerations

Our approach neither takes explicit account of interactions between genet fragments, nor explicit account of how particular arrangements of genet fragments may arise. Instead,

it asks merely the fitness benefit of such arrangements. This simple question alone is rich in possibilities. The answers to it should be of help in understanding other questions, such as optimal genet growth in relation to environmental variation, or 'optimal foraging' (Harper, 1985; de Kroon and Schieving, 1991; Cain, 1994; de Kroon and Hutchings, 1995).

The development here has focused on the effects on genet growth of particular spatial arrangements of genet fragments relative to patterns of spatial environmental heterogeneity. Moreover, the relative growth rates of the genet fragments under the various conditions are inputs to our analysis, and are used to predict the relative growth rate at the genet level. Little consideration has been given to how these various arrangements of genet fragments might arise. However, by being able to assess the merits of these arrangements, the stage is set for consideration of the kinds of plant growth patterns that would be most beneficial in a given setting (Harper, 1985; de Kroon and Schieving, 1991; Cain, 1994; de Kroon and Hutchings, 1995; Gersani *et al.*, 1998). These considerations can thus provide the basis for fitness assessment in models of the dynamics of clonal plants in spatially and temporally variable environments. The results here can also help in the development of physiological models in which the relative growth rates of genet fragments may evolve under given conditions with specified trade-offs. Accurate ways of assessing the resulting fitness of the genet and dissecting the contributions of its components, such as provided here, are essential.

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