

Clonal Plant Foraging: a Review and Simulation Study

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“This plant is peculiar in its way of shooting and originating; for from the trunk-like stock grows another slender root sideways, and on this again forms the fleshy part which contains the shoot from which the stalk springs.”

— Theophrastus
Enquiry into plants

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Abstract

Clonal plants present an interesting set of problems for biologists in that normal concepts of individuality do not apply to them. Plant foraging theory predicts how clonal plants (genetic individuals) place their subunits (ecological individuals) in their environment by combining plastic structural patterns with environmental conditions in an analogy to animal foraging theory. Some clonal plants present an additional difficulty in that they maintain connections between their subunits, allowing ecological individuals to share resources. In this thesis, a spatially explicit simulation was built to model plastic clonal growth and physiological integration in a spatially and temporally heterogeneous environment. It was found that a plastic foraging response was only advantageous in a spatially predictable environment, and that extreme plastic responses increased foraging success but led to decreased overall fitness due to increased intra-clonal competition. With respect to physiological integration, it was found that integration provided a net fitness benefit to clones in a temporally variable environment, and that the costs of integration can quickly become disadvantageous. Lastly, it was found that certain combinations of traits are advantageous only in restricted habitat types. A literature review regarding the prevalence of physiological integration as well as plastic responses in clonal plants was conducted, finding results for 73 species in 23 families. A true foraging response was observed in 33%, and facultative physiological integration was observed in 20% of the species surveyed. Predictions from the simulation's outcome are matched to empirical results both from the survey and from prior empiric studies. Trends were apparent such as the restriction of integration to resource-poor environments. Other predictions, such as the success of foraging in resource-poor environments, were confirmed. The results are discussed in light of animal foraging theory.

INTRODUCTION

“Modular growth, the rarity of senescence, curious reproductive schedules, the ability of a genet to function in bits, the absence of segregated germ plasm, and the effects that branching structure have on the capture of resources —all set modular organisms apart from those with unitary structure.”
John L. Harper (1985)

Clonal Plants

Clonal organisms are fundamentally different from other organisms in that they reproduce asexually by making copies of themselves. They can be found in groups as taxonomically diverse as flowering plants, cnidarians (jellyfish and corals), echinoderms, zooplankton, and fungi. In practice clonal reproduction and clonal growth are much the same. A given clonal subunit with enough resources will produce a copy of itself — a child — that grows off of its parent’s body. This process is analogous to normal growth (Schmid *et al.* 1995). Clonal organisms therefore consist of genetically identical repeating subunits, which in plants are called ramets. The collection of genetically identical ramets is called a genet, or single clone. One of the interesting points about clonal growth is that the subunits may or

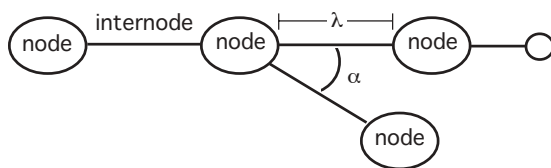


Figure 1.1 Simplified growth form of a clonal plant. The internode length is denoted by λ , which is constant throughout this clone. Ramets are indicated by “node,” and α shows the branching angle. The right-hand circle represents a young, unattached node on a developing internode. If empirically sampled, the branching probability would be $\phi = 0.5$ for this genet, since only one of the two non-terminal nodes branched. These three parameters (ϕ , α , λ) are Bell’s (1984) basic parameters that define a clonal growth form.

may not remain connected. For example, *Hydra* polyps detach and become free living. Because of their facultative connectiveness, clonal organisms generally provide a tough challenge to biologists attempting to define the basic unit of individuality. Genetically, a genet is a single individual. Ecologically speaking, each ramet is an individual. The definition

used will depend on the context in which the particular biologist is working — a population geneticist might count a genet as a single individual whereas a field ecologist might treat each ramet as an individual.

In plants there is another factor that complicates clonality. Clonal plants can be considered to be modular in their assembly. In a given tree, branches have twigs and leaves. Branches may also have other branches which themselves have twigs and leaves, leading to the definition of a module called “branch.” Clonal plants show a second-order modularity, with multiple stems or ramets (Alpert and Stuefer 1997).

In order to understand the benefits of clonality, first the basic biology of clonal plants will be introduced. This will then be supplemented by theoretical questions regarding plant foraging theory. Thereafter, a close examination of prior theoretical and empirical work will set the stage for the thesis’ research programme.

Architecture

The process by which a clone ramifies or spreads within its environment has been called dynamic morphology (Bell 1984). This concept takes into account developmental rules, environmental control, and ramet mortality. Bell (1984) defined clonal plants in terms of two building blocks: feeding sites (ramets) and spacers (stolons or underground rhizomes). This definition parallels the formulation of the building blocks of clonal plants as nodes and spacers (Sutherland and Stillman 1988). The difference between the two formulations is essentially the framework within which they were developed — Bell was primarily concerned with foraging whereas Sutherland and Stillman worked with plasticity. Functionally the definitions are equivalent. Bell additionally defined three variables that describe the

architecture of a given clone: the internode length (λ), the probability of branching (ϕ), and the angle of branching (α , see Figure 1.1). These are sufficient for determining a rigid growth form for any kind of clonal organism, and are the primary components of a species' dynamic morphology.

Plants' second-order modularity allows them to grow in multiple places at any given time (Alpert and Stuefer 1997). This gives them the "distinction" among all species of feeding simultaneously at many different locations (Bell 1984). This kind of growth has a cost to it, however, that is to be found in the construction and maintenance of connecting tissues (internodes). These costs have been modeled mathematically for clonal plants (de Kroon and Schieving 1991). The second order modularity of clones also allows them to spread laterally in their environment, which causes them to occupy an interesting middle position between highly mobile animals and immobile plants (Oborny and Cain 1997).

Each module will locally deplete the resources in its environment, creating a resource depletion zone, or RDZ (Harper 1985). Generally speaking, RDZ's will approximate spheres defined by the rate and direction at which a resource arrives at a point of consumption and the rate at which it is consumed (Harper 1985). If ramets are closely spaced, then their RDZ's may overlap, leading to a cost for the clone. This creates a sort of "ideal packing" problem, similar to those faced by crystallographers (Smith and Palmer 1976). There are two ways for a plant to avoid incurring this cost (Figure 1.2). The first is to grow in a highly linear fashion; to spread out with little branching. This has been called a "guerilla" strategy. The oppo-

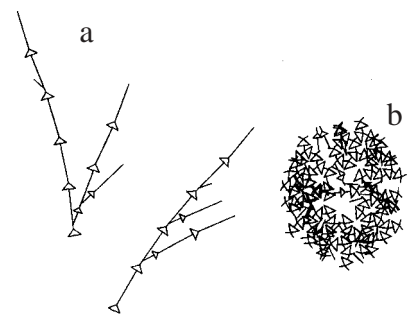


Figure 1.2 Comparison of guerilla (a) and phalanx (b) morphologies. Both diagrams represent the growth pattern of a single plant of the given type after eight "seasons" of growth. Triangles denote ramets; lines denote spacers. Taken from Bell (1984).

site growth form is highly clumped, termed a “phalanx” (Clegg 1978; Lovett Doust 1981b). These two poles of the growth spectrum have also been called runner and clump forms (Bell 1984). All clonal species occupy a spot on the continuum between the two morphological extremes.

Both growth forms can coexist within a single species. Cultivated *Trifolium repens*, white clover, displays two fundamental morphs: guerilla and phalanx (Sawada 1999). The phalanx morphs have two subtypes: the clonal subtype (more stolon investment) and the sexual subtype (more flower investment). The guerilla morphs show less integration and more plasticity, and are more advantageous in patchy sward environments. The clonal phalanxes dominate within patches whereas the sexual phalanxes are superior for interpatch migration. Therefore, both phalanx and guerilla forms coexist in sward environments.

Overall, clonal growth has both advantages and disadvantages. Clonality has associated costs, such as genetically depauperate population structures, with the commensurately increased risk of disease and higher inbreeding rates when individuals reproduce sexually. Clonal individuals also tend to accumulate mutations, both advantageous and deleterious, a problem which is particularly difficult for plants as they do not have a segregated germ line and all somatic mutations can be potentially carried into the next generation. It is easier for a connected clone to spread diseases such as parasites, viruii, or fungi among its ramets because it maintains inter-ramet connections with vascular flow. On the other hand, clonality provides for reproductive assurance in the absence of pollinators or potential mates. Clonality is a mode of reproduction that is analogous to simple growth, unlike sexual reproduction which only occurs once a certain nutritional threshold has been met (Schmid *et al.* 1995). It also allows an organism to simultaneously co-exist in

several places in its environment, as noted above, providing it with an advantage over its sessile relatives. The proliferation of modules in space may lower the probability of the genet's death by any one mortality factor (Hutchings 1999), except for pathogens which may spread more easily within a clone. A guerilla morphology may also allow a perennial clonal plant to persist in a highly disturbed environment when confronted with more competitive annual plants (Fahrig *et al.* 1994).

To review, clonal plants provide many interesting problems to biologists. Chief among these are the questions of the costs and benefits of second-order modularity. The basic architecture of clonal plants, which allows them to explore space differently from unitary organisms, fits into the continuum between phalanx and guerilla morphs. There are several advantages to clonality including reproductive assurance and ecological persistence. The thesis will focus on two further advantages, plasticity and physiological integration, which will be introduced below.

Plasticity

Developmental plasticity can be defined as a conditional growth response to particular environmental conditions. Plasticity itself (as opposed to rigidity), may be the result of selection (Oborny 1991). Under certain conditions, developmental plasticity may confer an advantage to an organism. There is an extensive literature pertaining to the evolution and benefits of plasticity (e.g. Thompson 1991). In clonal plants it has been shown for at least one species, *Trifolium repens*, that plasticity is heritable in the wild (Sackville Hamilton 1982). Any of Bell's three architectural parameters may show plastic responses. For example, *Ambrosia psilostachya* has been shown to selectively grow down a salinity gradient through plastic development of certain growth meristems while maintaining all other meristems in a state of dormancy (Salzman 1985). This exemplifies a branching frequency plasticity.

The example of *T. repens* above, with both guerilla and phalanx morphs, shows a classic case of internode length and branch angle plasticity. It has been suggested that a significant amount of plasticity in a clonal species will result in a compact growth form under good conditions (de Kroon and Hutchings 1995).

The concept of plasticity is inherently connected with resource allocation. The structures in which the plant chooses to invest its resources will dramatically affect its development. For example, de Kroon and Schieving (1990) showed with a mathematical model of resource allocation that a foraging growth form, where runners were short in favorable patches and long in unfavorable ones, would increase its branching intensity due to increased biomass allocation to the runners.

Plasticity can be costly, however, and a good review of the costs can be found in DeWitt *et al.* (1998). They are separated into maintenance, production, information acquisition, developmental instability, and genetic (linkage, pleiotropy, epistasis) costs. For example, clonal structures such as rhizomes and stolons consume resources, and the genes for clonality might be linked to other loci with deleterious alleles.

Oborny and Cain (1997) claim that the environmental heterogeneity faced by many clonal species suggests *a priori* that plasticity is important to their success. This claim is based on foraging theories that will be addressed below. To fully understand these theories, however, the essential concept of physiological integration must be introduced.

Physiological integration

During the growth of many clones, the connections between ramets will persist. These spacers (internodes) contain vascular tissue that is capable of transport-

ing nutrients and water in either direction. They are used to support the young daughter ramet during its development. If the connections persist throughout the life of the clone (which may be upwards of 43,600 years, Lynch *et al.* 1998), then the vascular tissue can continue sharing resources between ramets for the life of the clone. This sharing phenomenon is termed physiological integration. The extent of integration may range from zero (severed connections) to the sharing of all resources across all ramets in a genet. Numerous experiments have shown that the sharing may be bidirectional (e.g. Friedman and Alpert 1991), but Alpert (1991) claimed that architecture and integration can interact, each constraining the other. For example, vascular pathways need to connect to allow sharing. In some species each primary stolon is a separate physiological entity due to the species' developmental patterns in which vascular pathways are never bridged (Price *et al.* 1996). The following is an example where integration constrains morphology. Since integration alters the internal physiological states of the ramets, the ramets' dynamic morphology can change. Stuefer (1996) suggests that the flow of nutrients may suffer from certain constraints as to the distances, rates and directions that various nutrients may flow. These constraints may vary from nutrient to nutrient *within* the same clone, effectively making it very difficult to define the kind of sharing occurring in a given species. Despite this, certain efforts have been made to classify sharing intensities according to lifespan of ramets and spacers as well as ramet generational time (Jónsdóttir and Watson 1997). Different integration strategies will demonstrate the different relations between the three parameters.

Interestingly, resource sharing in plants is not limited to genetically identical individuals. Integration has been shown to occur between *Rhinanthus serotinus* individuals, through parasitic haustoria that are reciprocally attached (Prati *et al.* 1997). There is also a small body of literature dealing with strangler-fig (genus

Ficus) mosaic trees (e.g. Thomson *et al.* 1997) which can grow together naturally to form single individuals.

Physiological integration may proceed through two distinct mechanisms. It may follow a source-sink model (Münch 1930), as is frequently the case with photoassimilate and nutrient sharing that takes place through the phloem, or it may follow need, as is the case for water sharing via co-

hesion-tension (Marshall 1990). The latter may not involve any costs for the parent, as has been shown in *Fragaria chiloensis* (Alpert and Mooney 1986) and *Hydrocotyle bonariensis* (Evans and Whitney 1992). For a given ramet, leaves, inflorescences, roots, and other connected ramets may serve as sinks for nutrients originating in a given ramet. Resource acquisition for that ramet proceeds through leaves (light and carbon dioxide) and roots (water and nutrients) as well as influx from other ramets via stolons or rhizomes (Figure 1.3).

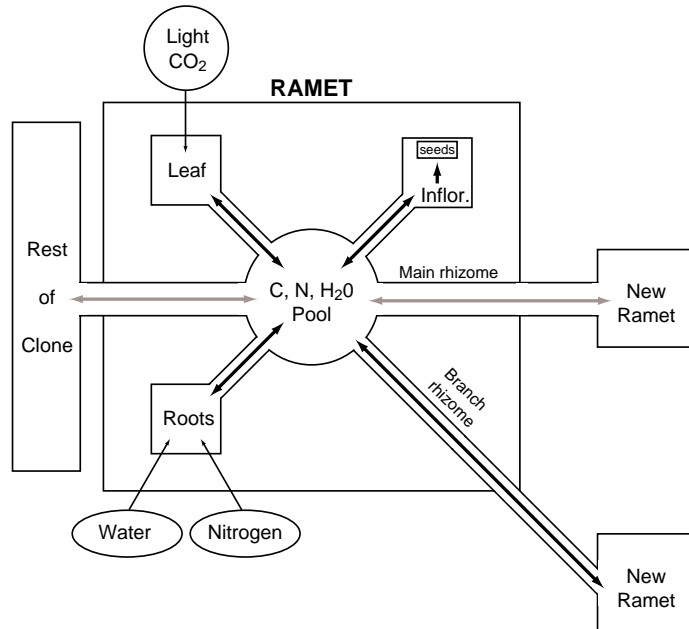


Figure 1.3 Diagram of potential source-sink relationships (thick black lines) for carbon (C), nitrogen (N), and water (H_2O) within a ramet near the leading edge of a rhizomatous clonal plant. Thick black lines indicate the direction of potential intraclonal translocation (integration) of these resources. Thin black lines indicate resource uptake pathways. Taken from Evans (1992).

Physiological integration is considered to be the ancestral state in the evolution of clonal organisms (Kelly 1995). It has been suggested many times (e.g. Jónsdóttir and Watson 1997) that physiological integration allows extended support of new ramets, recycling of harvested resources, and the regulation of intra-

clonal competition. Hartnett and Bazzaz (1985) also claim that integration allows the clone to average out environmental heterogeneity and local stress by buffering the stress applied to any single ramet. Hutchings and Price (1993) dispute the latter of these ideas. They suggest that physiological integration *does not* allow a clone to average out the effects of environmental variability. However, their results are largely based on work with a single species, *Glechoma hederacea*, and do not take into account the multiplicity of potential constraints proposed by Stuefer (1996). Additionally, they may not be approaching the question correctly. They showed that *G. hederacea* shows a local specialization and thus that ramets do not share the same internal resource state; hence there is no environmental averaging. The last step in that argument is faulty, as local specialization could occur despite nutrient sharing. In such a case nutrient sharing would not average environmental heterogeneity, but only buffer it somewhat.

Jónsdóttir and Watson (1997) conducted a small literature survey on physiological integration in clonal plants, and found that extensive integration seems to be found only in resource-poor environments. These data seem to support an earlier claim made by Bloom *et al.* (1985) that plants adjust their biomass allocation patterns in order to equalize growth limitation across ramets. The question of the benefits of physiological integration in clonal plants is still an open one, as there is only one well-characterized system (*G. hederacea*, all work that was conducted in M.J. Hutchings' lab). One aim of the thesis is to elucidate a potential benefit of integration within an evolutionary context that might apply to all clonal plants.

Some recent work has discussed the value of resource storage in the context of integration and evolution. For example, *Podophyllum peltatum* clones have only one active ramet which dies back each year, which is termed a pseudoannual habit.

A genet's underground rhizome will continue to grow and will give rise to another ramet at its tip the following year. It has been shown that the old root system still acquires resources from the soil and is an active participant in resource storage. Similar results have been shown in *Carex arenaria* (D'Hertefeldt and Jónsdóttir 1999).

The clonal literature has recently focused on the concept of sectoriality. This concept derives from the definition of an IPU, or integrated physiological unit (Watson and Casper 1984). Multiple IPU's in a single individual implies several sectors of the habit that are not integrated. The vascular architecture of plants, especially clonal plants, determines which parts form continuous physiological units. This in turn is largely directed by the local activity of meristems (Vuorisalo and Hutchings 1996). The direction of vascular flow also plays a large part in determining the organisation of IPU's within a clone (Marshall 1996). Generally speaking, non-clonal herbs are highly sectorial, with a large number of small IPU's, whereas clonal species have a high degree of integration (Marshall 1996). Sectoriality is under heavy phylogenetic constraint, but it does have benefits (Vuorisalo and Hutchings 1996). These may include the ability to limit mortality factors such as heavy metals or diseases to one part of the plant.

In review, physiological integration can occur for many nutrients between different individuals that are physically connected via standard resource transport pathways (xylem and phloem). The individuals involved may or may not be genetically related. Integration may provide fitness benefits to plants either by buffering out the environment or allowing a single individual to feed in many places in its environment at once by exploiting plants' second-order modularity. Connected individuals can form either one or many integrated physiological units (IPU's).

Integration has special application to plant foraging theory, as is introduced below.

Plant Foraging

Foraging as a biological concept derives from zoology. Foraging models attempt to describe how foraging organisms make decisions between possible feeding options in order to maximize their rate of energetic intake. Charnov's Marginal Value Theorem, or MVT, (1976) is the earliest and simplest model describing how foragers search for food in a patchy environment. In this sense, "patchy" refers to a spatially heterogeneous environment where resources occur in discrete clumps. This is differentiated from a case where resources are rare, but homogeneous throughout the environment. Since there are multiple resources, they may occur randomly (Figure 1.4a) or show some kind of structure either spatially or temporally in their location by either always co-locating (Figure 1.4b) or never co-locating (Figure 1.4c). The MVT predicts the amount of time that a forager should spend in a patch before moving on to the next patch. The decision to switch is made based on the rate of food intake and a complete knowledge of the environment. This is essentially a "hunt and seek" form of foraging, which is in contrast to

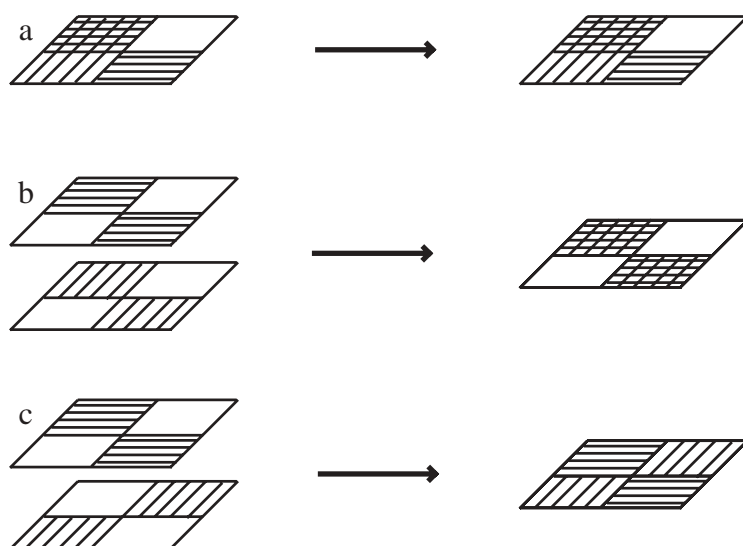


Figure 1.4 Representation of different types of heterogeneity caused by a patchy distribution of two resources. The occurrence of the resources may be independent (a), or show a positive (b) or negative (c) covariance in space or time. Open and shaded areas represent unfavourable (resource limitation) and favourable (no resource limitation) patches, respectively. The two types of shading refer to the availability of two different resources (e.g. light, nitrogen). Adapted from Stuefer (1996).

the opposite form of “sit and wait.” In the wild, foraging strategies fill the spectrum between these two poles.

Both Bell (1984) and Oborny (1991) have suggested that the search path of a mobile organism is analogous to the growth pattern of plants. Hölldobler and Moglich (1980) showed that the search path of a colony of *Pheidole militica*

ants can look very much like the growth pattern of certain trees (see Figure 1.5). The search path is in fact named “trunk-tree” because of this resemblance. This concept was further extended by López et al. (1994a, b) to include branch frequency. They also pointed out that, unlike plants, ants have alternative foraging strategies and are not constrained *a priori* as to the direction of trail construction. This similarity between how animals and plants explore space has led to the development of a conceptual foraging theory of plants that is a topic of active debate. The concept of plant foraging was first proposed by Grime (1979), and the word “foraging” was first used by Bell (1984) in his paper on dynamic morphology. The first mathematical formulation came six years later, when Kelly (1990) formulated a version of the MVT for the parasitic clonal plant *Cuscuta subinclusa*.

Although he did not use the term “foraging,” the process of plant foraging was first defined by Grime (1979) as the ability of plants to project leaves and roots into patches of high resource supply within the environment. This definition has been applied to all plants in terms of their placement of leaves, branches, and roots within their immediate space. For example, this placement becomes quite clear in

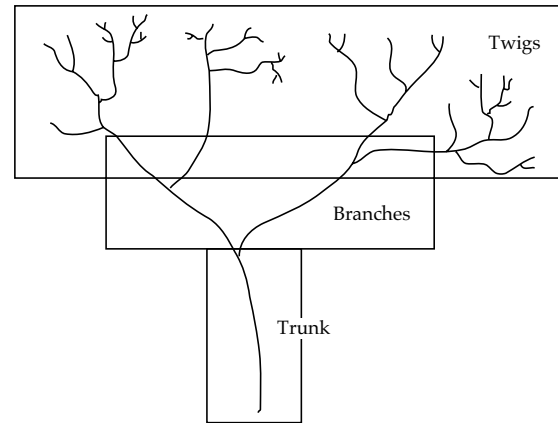


Figure 1.5 The foraging system of a *Pheidole militica* ant colony, adapted from Hölldobler and Moglich (1980). Note the topological and architectural resemblance to a tree.

the case of conifers when seen from above, as branches are layered highly non-randomly in such a way as to minimize self-shading (personal observation). It is extremely difficult to differentiate this kind of foraging from normal differential plant growth responses (i.e., growing towards an area of increased light simply because light increases growth). De Kroon and Hutchings (1995) defined foraging as “the processes whereby an organism searches, or ramifies within its habitat, which enhance its acquisition of essential resources.” This definition again is very broad and must be contrasted with an appropriate null model: the random placement of structures within the environment. Both of these definitions suffer from their generality and run the risk of adaptive story-telling (Oborny and Cain 1997).

The great parallel between plant and animal foraging lies in that not only do search paths look alike, but just as a single animal consumes all acquired resources and apportions them to its various organs, so does a single genet spread all resources found by its ramets between its various nodes. Physiological integration is a necessary part of this process. In a system without integration, however, adaptive foraging might work, as the genet will still benefit over evolutionary time by selectively placing ramets in better microenvironments.

These parallels have led to the use of the phrase “plant behavior” in the literature (reviewed by Silvertown 1998). Plant behavior combines both physiological and morphological plasticity into its definition, and focuses on ecological, physiological, and genetic aspects of these behaviors. It does not include many ontogenetic events such as germination. The timing of these events may be behavioral, however. The selective advantage of a particular behavior is separated from the presence of the behavior. The basic framework revolves around a 2-axis description of behavior in terms of sensitivity of the organism to the environment and the

complexity of response that can occur (Silvertown and Gordon 1989). For example, a highly complex plant behavior might involve the perception of some set of alternative states in the environment, with a response involving a signal by the plant to its environment, such as a change in flower color. This discipline is still in its infancy, however, and much is still debated.

Oborny (1991) defined foraging in terms of decision making, which parallels the definitions found in the zoological foraging literature. In her opinion, the decision is to switch between clump (phalanx) and runner (guerilla) growth forms. The main difference she posits is that the decisions made by plants foraging in a given environment are made over evolutionary time, with natural selection rather than cognition making the “decision” for when to switch patches by selecting for clones which are hardwired for the scale of plastic responses most appropriate to the environment. Interestingly enough, this may allow the plant to have the “complete knowledge” of the environment required by MVT assumptions. This knowledge is in the form of an understanding of the spatiotemporal predictability of the environment.

Kelly (1990) requires a pre-uptake investment in the acquisition for a given response to be called “foraging.” In animal systems, the forager must expend energy first by finding a patch and subsequently by processing the nutrients within it (i.e. opening nuts, digging up insects etc.) According to Kelly, a true foraging response involves an investment by the plant in the search process before any resources are acquired. This requirement comes from Charnov’s (1976) paper which first described the MVT. Such a response has currently been found in only two systems, *Cuscuta subinclusa* (dodder, Kelly 1990) and *Glechoma hederacea* (ground ivy, Birch and Hutchings 1994). However, because the foraging decision is an in-

herited developmental decision, this requirement should not be a concern (Oborny and Cain 1997). The investment is made on a different time scale.

The most recent definition of plant foraging comes from Oborny and Cain's excellent review of the subject (1997): "Plant foraging occurs when a plant exhibits any morphological plasticity that is selectively advantageous for resource acquisition at a particular spatiotemporal distribution of the resource." This definition holds several advantages over prior ones. First it implies spatiotemporal heterogeneity in the distribution of the resource. Secondly it invokes an evolutionary process for the development and optimization of foraging behavior. Lastly, it calls for a selective response by the plant to its environment in the form of plasticity. This definition assumes that the exploration and exploitation of the environment are mutually exclusive (spacers and nodes, respectively), and that the organism can switch between the two plastically with some feedback about the benefit of the switch. These conditions are fulfilled by phenotypic memory (Jablonka *et al.* 1995) and natural selection.

Harper (1977) distinguished between a developmental strategy and developmental tactics. A strategy is a long-term developmental program (under direct genetic control) whereas tactics are phenotypic variations within a strategy that are executed by individual plants. Plant foraging theory in an empiric sense is thus centrally concerned with tactics (Oborny 1991), whereas the evolution of plant foraging is concerned with strategy. The tactics exist essentially within the realm of phenotypic plasticity, and are "decided" by each ramet individually within a genet. Foraging is hypothesized to be most successful if each ramet can make developmental decisions independently of other ramets that may be experiencing other conditions (de Kroon and Schieving 1990). If this is the case, then physiologi-

cal integration, which averages the environment, reduces foraging efficiency (Oborny 1991). This prediction conflicts with other predictions of physiological integration theory, namely that it allows the genet to average out the environment's variation (e.g. Jónsdóttir and Watson 1997), but also that if each patch is composed of multiple resources that negatively co-vary (Figure 1.4c), integration allows the genet to place all ramets in favorable patches .

To test for “plant foraging” an appropriate null model is necessary (de Kroon and Hutchings 1995). Usually this takes the form of a random growth model, although it can also be a differential growth model where increased resource levels increase the growth rate. It must be noted however that field tests may be confounded due to physiological and morphological constraints on clonal growth (Oborny 1991, Oborny and Cain 1997).

It has been proposed that the scale of plant foraging can have a significant impact on the community structure of an area (Grime 1994). Dominant plants will forage on a coarse scale, whereas subordinate plants rely on precise fine scale foraging responses to acquire the resources they need from *in-between* the structures of the dominant plants. This conclusion is supported by morphological data from *Scirpus sylvaticus* (Grime *et al.* 1986, Crick and Grime 1987).

In review, plant foraging theory uses plants' plastic responses and draws on theories developed in the animal behavior literature to predict how plants explore space. The theory is especially interesting when applied to clonal plants, due to their second-order modularity. The simplest foraging theory that deals with patchy resources, the MVT, has been somewhat successful when applied to plants. Additionally, when a single genet in a heterogeneous environment selectively places its ramets in good patches and then shares resources between those ramets, it may be

able to use its ramets to specialize on the acquisition of globally poor but locally abundant resources. A division of labor has been created.

Division of labor

Division of labor theory comes from the economics literature. The theory was first formulated by Adam Smith in *Wealth of Nations* (1776). He defined division of labor as the complementary specialization of different units in a production system to perform different tasks necessary to the system as a whole. For the specialization to be profitable, it must increase the efficiency of production. In terms of clonal plants, division of labor requires both cooperation in the form of active stolons (with physiological integration), and specialization through morphological plasticity of individual ramets (Stuefer *et al.* 1996). It has been hypothesized that traits that allow the exploitation of environmental heterogeneity evolved on the basis of a spatial division of labor (Stuefer *et al.* 1996). This hypothesis may be problematic however, for the reasons explained below.

There are certain costs associated with division of labor. These costs may be “informational,” although it is unlikely. Due to their inherent modularity, plants have very few tasks that are divided. Unlike animals they do not have a plethora of specialized internal organs. There are certainly transport costs, which include the costs of maintenance of the transport infrastructure, i.e. internodes. There is also the cost of independence — the reduction in self-sufficiency that accompanies specialization. Should clone fragmentation occur, specialized ramets have very low fitness. The final cost is associated with temporal heterogeneity. It has been shown in greenhouse experiments on *Trifolium repens* that division of labor is unprofitable in temporally heterogeneous environments (Stuefer *et al.* 1996), i.e. that specialization of ramets is only advantageous in a spatially heterogeneous

environment, especially if resources co-vary negatively (see Figure 5c). Alpert and Stuefer (1997) hypothesize that in temporally variable situations, incomplete specialization would be more advantageous.

Essentially, only the possibility for a spatial division of labor has been shown for clonal plants. It has only been shown to occur in *T. repens* (Stuefer *et al.* 1996) in greenhouse experiments, but not in the field. There may be developmental constraints on a spatial division of labor in clonal plants (Alpert and Stuefer 1997), which would explain the results of Alpert (1996), where he failed to find morphological specialization in a field setting for *Fragaria chiloensis*.

To review, division of labor, by allowing a genet to specialize its ramets on resources that are locally abundant but globally scarce, may confer a benefit to clonal plants, and allow them to more fully profit from their second-order modularity. It depends on physiological integration (analogous to highways or other shipping routes) to be profitable. Although its possibility has been confirmed, its realization in the wild is still in doubt.

Models of Clonal Growth

“Plants ‘grown’ on a computer and defined by relatively few morphological parameters behave in a biologically interpretable way, as well as having the potential to produce realistic images of plant form. Such models provide a method of exploring the significance of plant growth patterns as evolutionary and ecological strategies.”
— Henry Ford (1987)

Because of the nature of the theoretical problems involving plant foraging theory, it lends itself quite readily to simulation studies. For example, there is an extensive literature dealing with how to graphically reproduce tree morphologies based on relatively few input parameters (e.g. Godin *et al.* 1999). The success of a

model is based on its ability to either reproduce or predict natural patterns. The quintessential example of the success of modelling can be seen in Hallé and Oldeman's (1970) classic work on the architectural forms of tropical trees, wherein they reproduce faithfully the growth patterns of a tremendous number of tropical trees using simple morphological parameters. In this section the basic theory of architectural models as well as prior applications will be discussed.

Definitions

Here I find it useful to distinguish between certain terms that are sometimes used interchangeably. A model is a generalized mathematical tool that attempts to explain phenomena parsimoniously by using simplifying assumptions. Models are frequently described mathematically. A simulation is a computer program designed to imitate some aspect of the natural world, be it physical, chemical, biological, etc. A simulation model is a simulation couched in a theoretical framework with variable parameters based on that framework or model.

Types of models

Generally speaking, models of clonality can be classified according to the way in which they typify growth rules, and the kinds of objects that they put into their "world." Any scientist constructing a simulation model of clonal growth has a fairly large number of decisions regarding the structure of the model that will have very significant effects on the kinds of questions that the model can be used to answer as well as the way in which it will answer those questions. A poorly constructed simulation model can yield results that are ridiculous from a wetware point of view (see Oborny and Cain's 1997 criticism of Sutherland and Stillman's 1988 paper).

Oborny and Cain (1997) review the kinds of models that are possible, as well as the structural rules that are necessary to consider when designing such a model. Generally speaking, models of clonal growth may be either architectural, generative, or descriptive. An architectural model aims at an algorithmic description of the spatial development of the plant in question. These are usually the simplest type of model, and are not spatially explicit. Bell (1979, 1986) gives examples. A generative model attempts to simulate the formation of individual growth patterns given a specific architecture. These are the most common kind of model, typified by the work of Sutherland and Stillman (1988), Oborny (1994b), and Evans and Cain (1995). These models usually aim to test some hypothesis such as the “foraging efficiency” of particular growth forms. Descriptive models, also referred to as spatial statistic models, are designed to analyze existing patterns of plants in the field and are rather rare. Generative models are the most interesting and potentially the most complex of these three types, as they may not only be descriptive, but prescriptive as well.

Generative models can themselves be broken down into two categories: single-clone and multi-clone models. A single-clone model will place only a single genet ancestor into its world and allow the plant to develop according to architectural rules. These models are usually analyzed in terms of the variation of one or more parameters such as environmental quality or changes in the architectural rules, and the output will be represented as a “typical run” of the model. Multi-clone models place several genets into the same world and allow them to interact during their growth, yielding a result that is much more realistic because it incorporates, at least partially, the biotic aspect of the clones’ environment (e.g. competition). Output from these models is presented in the same fashion.

Generative models are also characterized as general or specific (Sutherland and Stillman 1990). A specific model is one that is calibrated for or can only simulate one particular species. A general model is more abstracted and can simulate many species given the appropriate input parameters.

The growth rules used in generative models can also be characterized, as described by Oborny and Cain (1997). A particular growth rule must be designed following a series of choices. First, it may be deterministic or stochastic. A deterministic rule will always yield the same result given a set of starting conditions. Stochastic rules are based on some statistical distribution and are more variable, producing a range of outcomes from the same set of starting conditions. The distribution that is sampled to give the outcome must then be determined by the simulator, and can be drawn from empiric experimentation. Second, rules may also be either rigid or plastic. A rigid rule is unresponsive to environmental conditions whereas a plastic rule changes according to the environment of the plant. The difference between stochasticity and plasticity may be represented according to Table 1.1, which shows outcomes of all combinations of the above options.

Table 1.1 Outcomes of various growth rules in a simulation according to rule characteristics.

Nature of rule	Rigid	Plastic
Deterministic	Exactly the same, regardless of the environment	Exactly the same, based on the particular local environment
Stochastic	Based on a random distribution, regardless of the environment	Based on a random distribution chosen according to the local environment

Third, Bell (1986) defined rules as being either “sighted” or “blind,” which are defined in terms of the plant’s perception of the local environment. At first glance this distinction seems to be equivalent to that of “plastic” and “rigid,” but this is

not the case. Sighted refers to perception of the immediate environment of a particular ramet, but a plastic rule can use the environment of the plant as a whole. As mentioned above, plastic responses may allow the plant to “average out” nutrient-limited patches in its environment by removing the plant’s interaction with them (Oborny 1991). Temporal change in a growth rule (i.e., growth based on the age of the ramet) is called a nonstationary rule, whereas rules that do not alter over the course of the plant’s ageing process are termed stationary.

Models as predictive tools

Generative simulation models of clonal growth can serve several functions. Most commonly they are used as laboratories that can test which parameters are important for obtaining the observed growth form of plants (i.e., to derive the exact architectural rules) or to evaluate the function of these parameters in the effectiveness of the foraging strategy of clonal plants by using some sort of response variable such as the number of ramets in good patches (e.g. Sutherland and Stillman 1988).

Simulations can also be used as heuristic tools to provide a benchmark or a null model, much in the same way that the Hardy-Weinberg equilibrium equation is used currently in studies of genetic diversity. In the case of clonal plant growth, the use of simulation models as heuristic tools with respect to the final growth morphology or foraging efficiency would require either the quantification of the growth forms obtained from the models or field measures of environmental heterogeneity. To my knowledge, neither of these have been performed.

Simulations can be predictive as well. This is the case in some ecological studies such as that of Barkham and Hance (1982) who used a few rigid, deterministic

growth rules to predict a stable random clumping of daffodils (*Narcissus pseudonarcissus* L.) equivalent to observed field distributions. They altered the environmental parameters of their model to show the effects on the populations of an altered conservation regime in the coppice woodland occupied by these wild daffodils. They found that some of the local populations would die out, a prediction which was confirmed empirically following a 10-year study (Barkham 1992). As another example, Sutherland and Stillman (1990) predicted with their models that species with a shorter internode length will be more susceptible to the negative effects of ecological disturbance based on their models. This prediction has not yet been tested. Based on her models, Oborny (1994b) predicted that a foraging growth strategy (with plasticity of both branch frequency and internode lengths) would be much more efficient at low rates of environmental change.

Tested parameters

Previous studies have tested a number of growth parameters and their relative effects on the overall success rate of clones, which is usually measured in terms of the number of successfully placed ramets at the end of the simulation run (or runs if a stochastic model, Table 1.2).

Table 1.2 Parameters tested in previous clonal growth simulation studies, and their qualities which positively affect the success rate of the plant. S/L indicates a significant effect of plastic response of the internode length — short in good patches, and long in bad ones. H indicates a high branching frequency in good patches, which leads to aggregation in those patches. Please see text for details.

Study	Growth Form	Internode Length	Environmental Heterogeneity	Branch Angle	Branching Frequency	Notes
Cain <i>et al.</i> , 1996	No effect	S/L	Should be optimal for growth form	No effect	—	"Fast" vs. "Slow" growth forms
Oborny, 1994	—	S/L	Predictability is important	—	H	
Sutherland and Stillman, 1988	—	S/L	—	No effect	H	S/L result is questionable due to exaggerated responses

The overall growth form of a clonal plant has been tested only once by Cain *et al.* (1996), who tested the relative success of a “fast” and a “slow” growth form. The “fast” growth form is based on species such as *Trifolium repens* and *Hydrocotyle bonariensis* in which multiple generations of ramets actively acquire resources at any given moment. The “slow” growth form is based on species such as *Medeola virginiana* and *Solidago altissima* in which only the current or previous few generations of ramets acquire resources. They found no difference in the success rates of “fast” and “slow” clones.

All simulations to date that deal with clonal morphology have examined the effect of varying internode length. The first such study, conducted by Sutherland and Stillman (1988) concluded that plastic variation in the internode length (short in favorable patches, long in unfavorable patches) resulted in an aggregation of ramets in good sites. However, it was later found that the spacer length increases used in their model were artificially long — by a factor of five (de Kroon and Hutchings 1995). Oborny (1994b) showed that the same plastic response on a realistic scale provides a benefit to the clone by reducing the cost of foraging. The most recent simulation by Cain *et al.* (1996) showed that the same plastic response used by Sutherland and Stillman (1988), but with realistic values for the internode length variation, can provide a fitness benefit. Shortened internode lengths in good patches allows aggregation in good patches, supporting Sutherland and Stillman (1988). When the benefit reaches significant levels, there is also a cost to the response, as per Oborny (1994b). A non-plastic or fixed internode length may provide a fitness benefit by allowing for a continuous search of the environment (de Kroon and Hutchings 1995).

Only two studies so far have investigated the role of environmental heterogeneity on the success of clones. Oborny (1994b) found that the adaptive nature of a

growth strategy largely depends on environmental predictability. In poorly predictable environments a “sit and wait” phalanx growth strategy seems to be beneficial, whereas in highly predictable environments a true foraging guerilla growth strategy provides the highest benefit. Cain *et al.* (1996) found that there is an optimal patch size for a particular clonal architecture. This result has interesting implications in terms of using clonal plants as bioindicators for the scale heterogeneity in a given environment.

The two studies to date that examined branching angle plasticity (Cain *et al.* 1996, Sutherland and Stillman 1988) found that varying the branch angle provides no benefit to a clonal plant. Additionally, many plants may be developmentally or morphologically constrained with respect to this parameter, rendering further modeling uninteresting. Both studies that have examined branching frequency effects (Oborny 1994b, Sutherland and Stillman 1988) have found that a higher branching frequency in good patches promotes the aggregation of ramets. This may entail a cost for the clone, due to intra-clonal competition.

Other results

The simulations summarized above have also tested the effects of other parameters. Oborny (1994b) showed the growth form of a clone cannot be determined from its growth rules due to genotype (architecture) — environment interactions. A particular genotype can grow to wildly varying forms in different environments, especially if the genotype is highly plastic. She also related the information content of the environment in terms of numbers of patches and their spatial predictability. These are the only environmental parameters that have been explicitly related to plant foraging success. Cain *et al.* (1996) found that including ramet mortality in the simulation reduces the cost of intracolonial competition.

Critiques of current simulations

Unfortunately, most simulations of clonal growth are either not constrained by realistic responses, or not truly spatially explicit (Cain *et al.* 1996). Many models also do not include a component of temporal variation of patches. Oborny (1994b) did, but her patch turnover values were completely arbitrary and no correlation with actual field conditions were reported. It has been shown that small amounts of temporal heterogeneity dramatically reduce the efficiency of the growth form which is plastic both for branching frequency and spacer length (Oborny and Cain 1997). Additionally, ramets themselves may deplete resources and change patch turnover rates. No current models take into account RDZ's (resource depletion zones, *sensu* Harper (1985), or RDZ creation rates. This is a serious oversight for those models that attempt to include intraclonal competition costs (e.g. Oborny 1994b).

To date, the predictions from all models of plant foraging remain unrelated to empirical data. Cain *et al.* (1996) calibrated their models with empirical data, but they failed to compare their results with field ecological data. Most authors consider it satisfactory to show a "typical output." However, results should be quantified to allow for a rigorous method of comparison with empiric data. Birch and Hutchings (1992a, b) use a plastochron index to quantify the rate of stolon development. A plastochron is the amount of time between repetitions in the growth pattern (Erickson and Michelini 1957). This is a good start in developing null models of clonal growth, but is unhelpful with respect to the topology of growth. Cain *et al.* (1996) calculated a Morisita index (developed by Morisita 1959) from the outcome of their models. This index is independent of ramet density and quantifies the spatial clumping of ramets. It varies from zero to one when ramets are randomly distributed, and is greater than one when ramets are clumped. This index

goes a long ways towards the quantification of the results of a theoretical model but remains independent of topology. Fitter (1987) borrowed a topology quantification procedure from the river drainage basin literature and used it to describe root systems. Such a method could be applied to the topology of stolon or rhizome branching systems. I propose to rectify the problem of lack of topological outputs by quantifying the growth forms of the models I develop below using Fitter's method.

Evolutionary predictions

All models to date have attempted to measure the success of various growth forms in terms of a variable that is correlated with fitness: the percentage of ramets placed in good patches. Any trait affecting fitness that is heritable is subject to selection. Since the architecture of a clonal plant is developmentally constrained, both in terms of growth rules and of allowable amounts of plasticity, plant growth forms will be selected for. The problem with evolutionary arguments involving clonal plants is the plants' modularity. Because of their second order modularity (Alpert and Stuefer 1997), any selective pressures working on clonal plants will necessarily act in a hierarchical manner (Tuomi and Vuorisalo 1989b). The difficulty lies in that the individual modules may be partially, but not fully dependent. They have identical genomes despite potential physical separation. The line between individual and group selection becomes blurred, leading to Tuomi and Vuorisalo's (1989a) suggestion that "interactive units (modules, organisms, and groups) may provide potential levels of phenotypic selection if they have a distinguishable causal impact on reproduction at the level of reproductive units." It should also be noted that selection cannot act on plastic responses if the environment does not allow the full expression of a developmental program, even if that program is advantageous (Oborny 1994b).

Oborny (1994b) and de Kroon and Hutchings (1995) have suggested that the profitability of any level of morphological plasticity is dependent on spatiotemporal heterogeneity in resource supply and that growth forms with varying levels of plasticity will have varying levels of success under a particular spatiotemporal heterogeneity regime. Oborny (1994b) further suggests that plastic growth forms are not necessarily any better than rigid ones — in a highly temporally heterogeneous environment, a sit and wait approach to foraging may be preferred. The choice of which strategy to employ, hunt and seek vs. sit and wait, is contingent upon the amount of environmental predictability (Stuefer 1996).

Empiric Data on Clonal Growth

Now that the prior modelling work in this field has been described, the focus can be shifted to the empiric work that has been done in four model systems which represent the best studied clonal plants in order to see how the modelling work matches up with the wetware.

Fragaria chiloensis

The beach strawberry *F. chiloensis* (L.) Duchesne is found primarily in the sand dunes immediately abutting the Pacific Ocean of North America and Chile. It provides an interesting system because its stolons grow above-ground, ramets are easy to manipulate due to the nature of the substrate, and its environment is extremely simple. It grows primarily in a guerilla morphology. Stolons can reach over 100 meters in length (Alpert *et al.* 1993). Essentially, the only things growing where it is found are *Artemisia pycnocephala* shrubs, nitrogen-fixing lupine shrubs (*Lupinus arboreus*), and beach grasses. This layout provides a heterogeneous environment, typified by two resources that negatively co-vary (see Figure 1.5c): light

and nitrogen (Alpert and Mooney 1996). Underneath the lupine bushes there is nitrogen but little light, and in the open there is light but no nitrogen.

There is evidence to suggest that *F. chiloensis* engages in plastic foraging. Alpert and Mooney (1986) used a radiolabeled compound to show that the ramets of *F. chiloensis* maintain active connections that reciprocally transport nitrogen compounds and photosynthates (sugars) between ramets. They also showed that shade induces the import of photosynthates by ramets. Integrated siblings convert a mosaic of bad patches, where each has a lethal scarcity of a critical resource, into a mosaic of good patches (Alpert and Mooney 1986). The patch values must be high for this to occur, however (Friedman and Alpert 1991). A study comparing genotypes from a beach population and a nearby grassland population (where resources are more plentiful, and more homogeneous) showed that individuals from different environments are selected on for the amount of integration they display, with grassland individuals being more selfish (Alpert 1999).

Alpert (1991) showed in the greenhouse that in bad patches *F. chiloensis* ramets will allocate resources towards the growth of new stolons and ramets, whereas in a good patch allocation will be both towards the growth of new stolons and ramets as well as to growth of the primary ramet. This translates into an increased internode length in bad patches, predicted by the simulation studies discussed above.

A single ramet of *F. chiloensis* will adapt to acquire the resource that is the most scarce in its local environment — following the so-called optimal allocation theorem. Due to physiological integration, connected ramets will adapt to acquire what is globally the rarest resource (Friedman and Alpert 1991). This implies a plastic foraging response on the part of the integrated plant.

There is conflicting evidence as to the effects of heterogeneity on the growth of *F. chiloensis*. Alpert (1991) claims that heterogeneity between ramets increases growth. However, in 1996 he claimed following a greenhouse study that there was no evidence for differences in nitrogen-sharing patterns across different levels of heterogeneity (contrast between patches); generally speaking transport remained acropetal (from mother to daughter). This may be due to sampling at scales of heterogeneity that are not perceived by the plant (Kolasa and Rollo 1991).

Glechoma hederacea

The perennial ground ivy *Glechoma hederacea* L. also provides a good study system for investigating clonal foraging. Like *F. chiloensis*, its stolons are above-ground and remain connected, and it too shows extensive plasticity. Under low resource supply it develops reduced branching, a longer internode length, and alters its biomass allocation (Hutchings 1988). Birch and Hutchings (1994) showed that its ramets will differentiate to specialize in the uptake of a certain resource (e.g. light, minerals). Also like *F. chiloensis*, a heterogeneous environment increases growth (Birch and Hutchings 1994). Its resource sharing between ramets is also acropetal (Price and Hutchings 1992b, Price *et al.* 1992). Under conditions of poor resource availability, it will extend its internode lengths, again supporting prior predictions (Slade and Hutchings 1987a, b, c).

There are, however, some differences between *G. hederacea* and *F. chiloensis*. *G. hederacea* is capable of assuming either guerilla or phalanx morphologies if resources are abundant or limited, respectively (Hutchings 1988). This supports the predictions of Hutchings and de Kroon (1994), as well as those of the simulations of Sutherland and Stillman (1988), Oborny (1994b) and Cain *et al.* (1996) re-

garding the benefits of plasticity. Lastly, the scale of heterogeneity that is perceived by *G. hederacea* has been determined (Wijesinghe and Hutchings 1997).

Hydrocotyle bonariensis

Hydrocotyle bonariensis, the largeleaf pennywort, lives on southeastern beaches of the United States. It shares some features in common with the two species above. Rhizomes persist over the life of the clone, and there is significant resource sharing between ramets (Evans 1988, 1991). Ramet morphology is rather plastic (Evans 1992), with increased plasticity in highly heterogeneous environments (Evans and Cain (1995). Internode lengths increase in bad patches (Evans and Cain 1995).

Unlike the systems investigated above, *H. bonariensis*' branching frequency decreases in bad patches (Evans and Cain 1995), which is another prediction of the simulations of Sutherland and Stillman (1988) and Oborny (1994b). *H. bonariensis* shows one astounding response that is highly suggestive of an active foraging response. In an experiment conducted by Evans and Cain (1995) where *H. bonariensis* was induced to grow towards a bad patch that was low in resources due to depletion by a dune grass species (creating a RDZ), rhizomes actually veered away from the RDZ! They also found that foraging-related traits can be expressed differently in response to above- or below-ground resource availability. These results make this species a good candidate for the description of an active plant foraging response.

Cuscuta spp.

Some very interesting work has been performed on a rather odd kind of clonal plant: dodder (genus *Cuscuta*). Dodder is a parasite that shows a typical coiling

response around a branch or stem of a host if it decides to accept that host. Alternatively, the growing stolon will continue on without coiling, indicating rejection. This leads to wonderful opportunities for experimentation. It has been shown that dodder is more likely to accept a host with a good nutritional status (Kelly 1992). Additionally, dodder is the only species for which a quantified foraging model has been created (Kelly 1990).

Conclusions

From the review of model systems above, we can reach several conclusions. It appears that the relative contribution of ramet branching to a clone's ability to forage decreases with high physiological integration, and that a plastic foraging response is not necessarily linked to ramet independence (Evans and Cain 1995). The bulk of the spatially explicit tests were created by using patches with a high excess of nutrient availability — a condition that fails to accurately mimic natural conditions. This would tend to exaggerate the reports of a foraging response. It would also increase the value of physiological integration (Friedman and Alpert 1996).

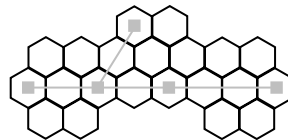
Focus of the Thesis

Current deficiencies in the literature

Cain *et al.* (1996) and Oborny and Cain (1997) each cite the lack of spatially explicit models that include temporal heterogeneity that are based on biological data. Oborny and Cain (1997) also cite the need for models that deal with fitness — to date all models have reported the number of “successfully placed” ramets.

Plans for the simulation

I propose to construct a spatially-explicit generative simulation that uses spatiotemporal heterogeneity of two resources and is built on a fitness system. The simulation model will be a general, stochastic, plastic, sighted, single-clone, stationary model. The resources collected from patches will be translated directly into plant fitness units. The model will then be extended to include physiological integration via fitness point sharing between ramets. I plan to build the model keeping a degree of biological realism based on the extensive data on *F. chiloensis* and *G. hederacea* collected by Peter Alpert, Michael Hutchings and their co-workers. The simulation's results will be gauged against the results of a literature review that examines the available data on plastic responses of internodes, clonal growth parameter values, and physiological integration data. The model will then be generalized to other plants, following a procedure similar to that used by Cain *et al.* (1996).



MATERIALS AND METHODS

“Each branch or leaf of a tree may be regarded as merely engrafted or inoculated upon it, and therefore as a tree with an existence of its own, simply attached to another from which it nourishes itself.”

— Immanuel Kant

Kritik der teleologischen Urteilskraft

Simulation

Construction and Programming

The simulation program, IntegraClone 1.0, was designed to provide a simulation of the growth morphology of a generic clonal plant. It places a single genet within a specified environment and creates the clone's growth via a stochastic Markov chain simulation. The program was written and designed following Object Oriented Programming (OOP) principles. This architecture allows the code to be easily modified and expanded, without requiring extensive rewriting. OOP architectures also allow programs to be built in a modular fashion, where each module acts independently of the manner in which the other modules act. Each module is responsible for its own behavior, and a particular module's internal behavior can be altered without any direct repercussions on the rest of the program. A module can be anything including a button on-screen, a window, a ramet or a particular simulation run. All code was written using CodeWarrior Pro 5 as a compiler with the PowerPlant 1.9.3 application framework. All development work was performed on a Powerbook 1400cs/133 running Macintosh OS 8.6. The code was written in ANSI C++. Fully commented code for the program appears on the accompanying CD-ROM.

The first part of the program implemented was the visual interface, as is common practice in graphical user interface (GUI) environments such as the Macintosh

OS. Part of the interface was the retrieval and display of parameters. The second step was to implement the world environment. Ramets were then created to be placed in it. The visual interface was then checked against small, arbitrarily created (i.e. hardwired) clonal structures to insure that it was correctly reporting clonal architectures. Then the environment's patchiness with a single resource was added. This allowed for the next step: the creation of actual clonal growth, wherein a ramet could produce a copy of itself based on its internal resource state. From there a second resource was added to the environment; the plastic responses of ramets soon followed. The last step necessary for the biological programming was the implementation of a physiological integration algorithm to share resources between plants. To allow the program to execute experiments, the program was given file I/O capacity to read a series of parameters from a text file, automate the processing of those simulations, and output the results to a different text file. This last step was performed in order to simplify the data collection process.

The fitness system

IntegraClone's fitness system deserves special attention. Part of the user inputs are fitness values that are used for the costs of ramet maintenance, reproduction, and integration, as well as for the amounts of each resource that are available in a given patch. A point-based system was chosen because it allows all costs and resource intakes to be standardized by the user. They can be input as ratios of each other with potentially very large values, allowing them to have whatever relations the user desires. Additionally it facilitates analysis by allowing them to be compressed into unitless values through division. In a rich environment, a genet will usually acquire excess fitness. Those "extra" fitness points in a true clonal plant could be allocated to sexual reproduction. In that sense the fitness points allow a

measure of evolutionary success that is different from, though related to, the number of ramets.

Simulation Process

For a given run of the simulation, the specific process executed was as follows.

First the parameters (see Table 2.1) are read from the particular input source, be it

Table 2.1 Numerical input parameters used by the simulation program IntegraClone, listed with the units of measure. The default value and tested range columns refer to the simulation runs that were conducted. Please see textual descriptions of simulation and experiments for more detail.

Parameter	Description	Units	Default Value	Tested Range
α Branch angle	Angle of deviation from main stolon axis for lateral ramets	degrees ($^{\circ}$)	60	
ϕ Branch probability	Probability of creation of lateral ramets	none	0.50	
ϕ_p Branch probability plasticity factor	Amount by which ϕ can change due to local environmental conditions	none	0	0 - 0.50
λ Internode length	Length of an internode	hexagons	2	
λ_p Internode length plasticity factor	Amount by which λ can change due to local environmental conditions	hexagons	0	0, 1
ξ_m Maintenance cost	Cost of maintaining a ramet for one time step; charged to both resource A and B pools	fitness points	15	
ξ_r Reproduction cost	Cost of creating a new daughter ramet; charged to both resource A and B pools	fitness points	20	
ξ_i Integration cost	Cost of integrating resources; charged to both resource A and B pools	fitness points per unit of λ	0	0-5
F_A Resource A frequency	Frequency of high-quality resource A patches in the environment	none	0.33	0.1, 0.33
F_B Resource B frequency	Frequency of high-quality resource B patches in the environment	none	0.33	0.1, 0.33
Q_H High patch quality	Amount of a given resource available in a high-quality patch each turn	fitness points	20	
Q_L Low patch quality	Amount of a given resource available in a low-quality patch each turn	fitness points	16	
T Patch turnover rate	Probability per turn of a given patch changing its resource content values between Q_H and Q_L	none	0	0 - 0.10
S Patch size	The radius of a patch	hexagons	3	1, 3
W World width	The size of one dimension of the square world	hexagons	150	
t Time steps	The duration of the simulation	none	100	

the visual interface or a text file. Then a new world is created with a hexagonal grid in which patches of the specified size are assigned resource levels based on patch frequency inputs. The two resources, A and B, can exist in the environment at two levels: high (Q_H) and low (Q_L). Patch values are assigned based on the input patch frequencies (F_A and F_B). If a given patch meets the input probability it acquires a high resource level for that resource. There is a spatial covariance algorithm to insure that both resources can have a spatial covariance (as per Figure 2.1) if requested by the user. A patch size of one indicates a patch of one hexagon, a size of two indicates a squarish cluster with a radius of two, and a size of three

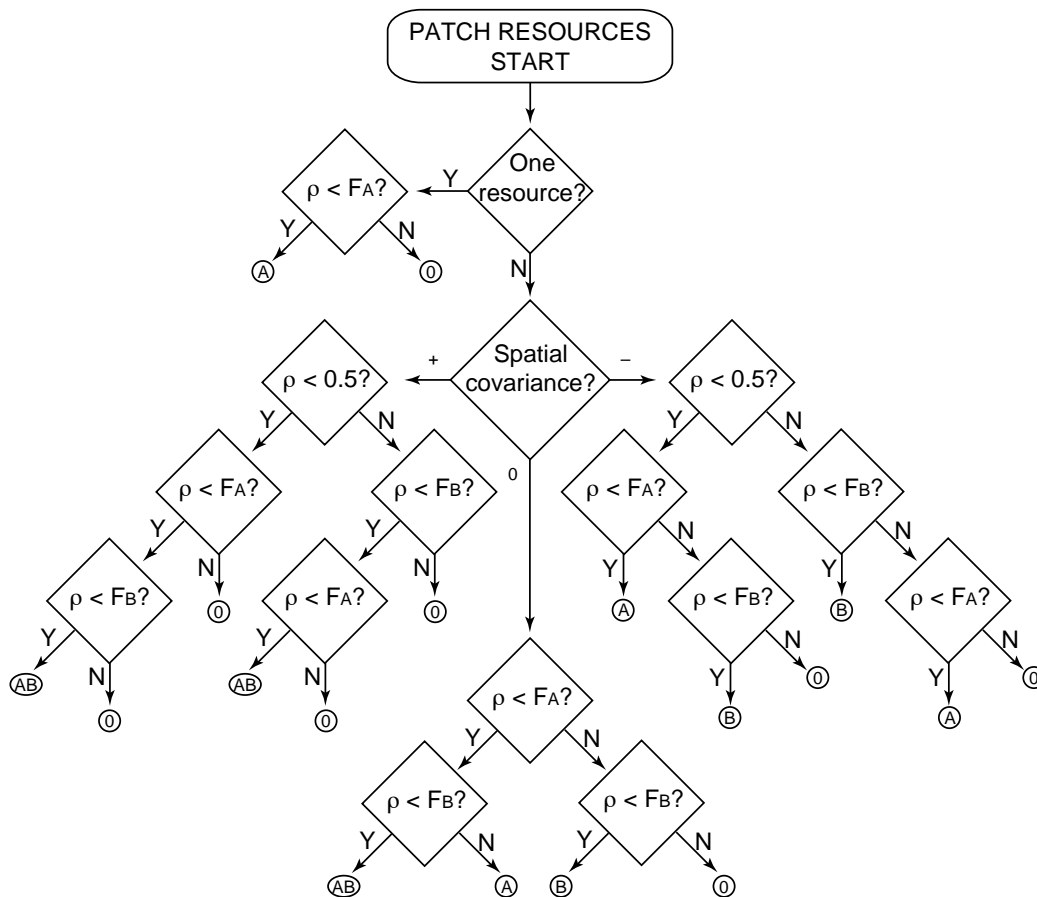


Figure 2.1 Flowchart describing the patch resource spatial covariance algorithm. The algorithm insures that, given two resource types, patches of both resources will colocalize in space appropriately: either always together (positive covariance), never together (negative covariance), or independently of each other (no covariance). The parameters F_A and F_B are user-input, and ρ indicates a random number generated each time a ρ appears in the flowchart.

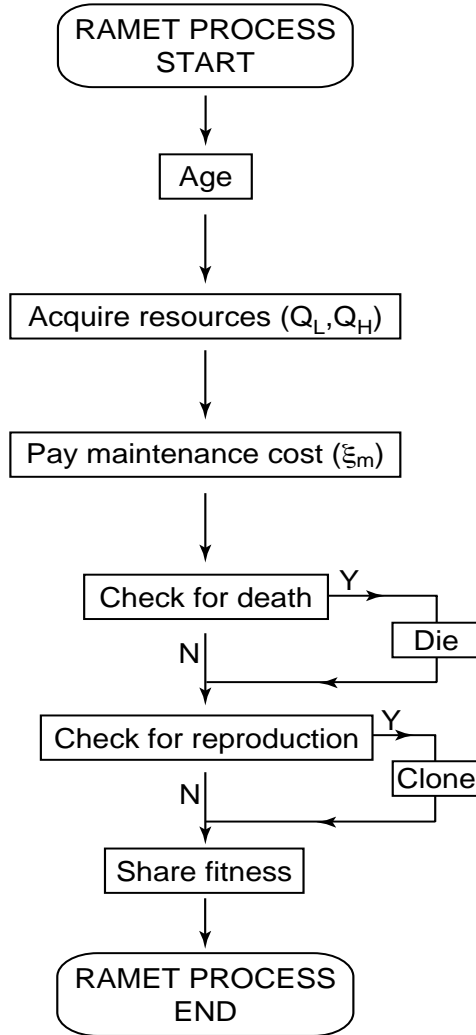


Figure 2.2 Flowchart describing the processing of a single ramet. The program recursively traces through the entire clone to process all ramets, from child to parent.

marks a squarish cluster with a radius of three. A mother ramet is created in the middle of the world.

A time step counter is then initiated to begin temporal processing and count the appropriate number of time steps (t) until the end of the simulation. During each time step, the clone is parsed recursively from daughter to mother. Each ramet is then given an opportunity to acquire resources from its environment, clone itself if possible, and die if necessary (see Figure 2.2). At the end of the time step the clone's resources are physiologically integrated via a simple averaging algorithm (if required). The patches are then processed one at a time and are given a chance to “turn over” — to change resources levels based on the probability input of the user (T).

When all time steps have been processed, the clone is parsed recursively once more to determine its excess fitness (W_r , the pool of fitness points not spent on maintenance or reproduction), ramet survival rate (d), placement success rate (s), and certain topological features such as its magnitude (M), longest path length (P_m), average internode length (l), and average branch number (b). The ramet sur-

vival rate is the percentage of ramets remaining alive at the end of the simulation. The placement success rate (s) is calculated as follows:

$$s = \frac{N_{AB} + \frac{1}{2}N_A + \frac{1}{2}N_B}{N_{tot}} \quad (2.1)$$

In equation (2.1) N_{AB} is the number of live ramets in a patch with high levels of both resources; N_A is the number of live ramets in a patch with a high level of A and a low level of B, and vice-versa for N_B . N_{tot} is the total number of live ramets. The magnitude (m) of the clone is equivalent to the total number of terminal ramets (ramets with no daughters). The longest path length (P_m) is the largest number of internodes between the mother ramet and a terminal daughter in the tree. The average internode length (l) is calculated by dividing the sum of the internode distances in hex-

agonal units by the number of internodes. Finally, the average branch number (b) is calculated by dividing the total number of daughters per ramet by the number of non-terminal ramets. All output parameters are summarized in

Table 2.2 Numerical output parameters used by the simulation program IntegraClone, listed with the units of measure. Please see textual description of simulation for more detail.

Parameter	Description	Units
W_t Total fitness	Total genet fitness	fitness points
m Magnitude	Fitter magnitude of clonal branching structure	none
p_m Path length	Largest number of internodes between mother ramet and a child	internodes
l Average λ	Mean λ averaged over all internodes in genet	hexagons
b Average branch number	Mean number of children per ramet	ramets
s Success rate	Frequency of placement of ramets in good patches	none
d Survival rate	Percentage of ramets surviving at end of simulation run	none
N_g Ramet number	Total number of ramets in genet	ramets

Table 2.2.

The life of a ramet

To put the simulation process into a different and perhaps more biological perspective, it is helpful to go through a ramet's-eye view of the simulation. The description that follows applies to all ramets, including the mother ramet. Two important events happen at birth. First, the ramet's internal fitness pool is set to zero. Second, the ramet's branching fate is decided stochastically based on the user input branch frequency (ϕ) and plasticity values (ϕ_p). Making this decision at birth is supported by empiric data. Some clonal studies (e.g. Salzman 1985) have shown that ramets are born with dormant lateral meristems which can then become active later in the ramet's life. In those systems investigated it was found that a particular ramet will be unable to create new lateral meristems during its lifetime. In this case, the new child ramet checks its environment, adjusts the base branch frequency value up by the plasticity factor if in a good environment, and down by the same factor if in a bad environment, and rolls the dice to decide if it has lateral meristems. It is assumed that the ramet knows if it is in a one- or two-resource environment; short-term phenotypic memory (*sensu* Jablonka *et al.* 1995) and long term selective pressures (Oborny 1991) validate this assumption.

During each turn, a ramet can perform a number of different tasks (Figure 2.2). First it acquires resources from its environment. It queries the patch that it finds itself in, and adds the appropriate number of fitness points (either the high or low values, Q_H and Q_L) for each resource to its internal storage. It then pays the user-input maintenance cost (ξ_m) in fitness points, by subtracting those from its storage. It then compares its fitness level with the cost of clonal reproduction (ξ_r); if it has enough points, it spends them on creating a child. If the daughter is the ramet's first, then it is created along the pre-existing axis of growth that is established by the ramet and its parent. If the ramet already has a single daughter and is inca-

pable of branching then it spends no fitness points on reproduction. Alternatively, if it is capable of branching then it can go on to form a second (or third) daughter (see Figure 2.3). The direction, left or right, compared with the prior growth axis is determined by a coin toss. In all cases when cloning itself, the distance between the ramet and its daughter is determined by taking the base internode length (λ) and modifying it by

the plasticity factor (λ_p); up if the mother is in a poor patch and down if in a good patch. Daughters whose placement would be either on top of another pre-existing ramet or outside of the world's bounds are not created, and the ramet is not charged for them.

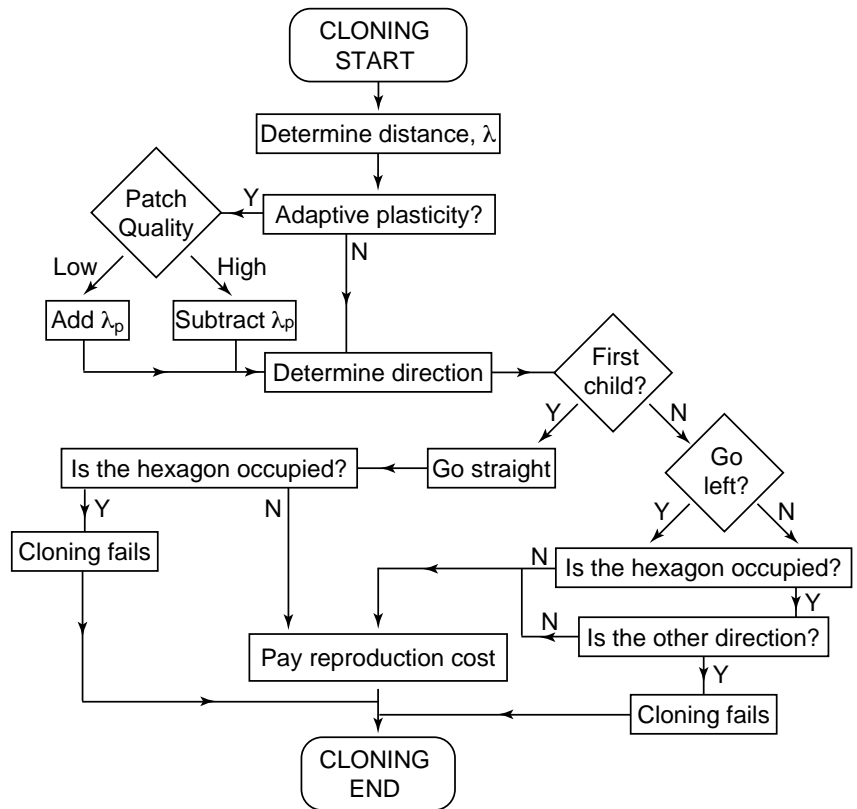


Figure 2.3 Flowchart describing the process of ramet cloning. The parameters λ and λ_p are user-input. The patch quality of the parent ramet determines the internode length, λ . The first child is produced following the primary stolon's axis; the second and third child go left and right off of the axis. The decision to go left or right is a coin toss.

During the physiological integration process the ramet reserves a single time step's maintenance cost and gives up any excess fitness that it has to contribute to the genet's pool. When that pool has been calculated for the entire genet, the cost of integration (ξ_i) is subtracted once *for each unit of stolon length* in the genet. The

points remaining in the communal pool are distributed equitably to all ramets, with any odd points coming from round-off error being distributed acropetally to the terminal children. If the pool is negative, then all ramets are charged appropriately, with costs tending to remain basipetal.

Software testing

The model was tested for accuracy during development to insure that all implemented features worked correctly. As each feature was added it was tested by step-wise debugging while monitoring all variables to insure that the code was correct.

Software use

The simulation program was executed and all data were collected on two dozen PowerMacintosh 7300/150 computers all running the same installation of Mac OS 8.6, over a period of several days.

Experiments

All experiments conducted were designed as simple two-, three-, or four- factor experiments, where each factor occurred at two or three discrete levels. The first experiments conducted were designed to replicate prior clonal modeling results that do not include physiological integration. An additional experiment was conducted to replicate some interesting recent empirical work by Alpert (1999). Lastly some tests of the integration system were performed. For all runs the following parameters were kept constant: α , ξ_m , ξ_r , Q_H , Q_L , W , and t (Table 2.1). It was decided that α would not be tested due to the nature of the world environment. On a hexagonal grid only branching angles of 60° and 120° are possible, and angles of 120° were not reported by any of the studies used in the literature review. The

rest of the parameters were assigned default values for those experiments in which they were not varied. They are ϕ , ϕ_p , λ , λ_p , integration and ξ_i , spatial covariance, F_A and F_B , Q_H and Q_L , T , and P . The values for these and the constant parameters listed above appear in full in Table 2.1.

The experiments designed to replicate prior modelling results addressed the following questions. First, what is the effectiveness of the foraging response, and which components contribute most? A test of the foraging response was conducted by varying the branch frequency plasticity ($\phi_p = 0, 0.1, 0.25, 0.5$) and the internode length plasticity ($\lambda_p = 0, 1$) independently at the indicated levels. It was predicted that the highest levels of the plasticity factors would produce the highest foraging success rates (s), and a higher fitness (W_t). Since the patch frequencies are less than 0.5, the clone morphologies should become slightly more guerilla for plastic clones.

Second, is the foraging response effective in a temporally variable environment? A test of the foraging response against turnover rate was then conducted by varying branch frequency plasticity ($\phi_p = 0, 0.25, 0.5$) and internode length plasticity ($\lambda_p = 0, 1$) independently. An additional independent variable was added by varying the patch turnover rate ($T = 0, 0.01, 0.05, 0.10$). It was predicted that higher turnover rates would reduce the foraging efficiency (s), and the overall fitness (W_t).

Third, does the scale of spatial heterogeneity affect the foraging response? The foraging response with branch frequency ($\phi_p = 0, 0.25$), and internode length ($\lambda_p = 0, 1$), was tested with the patch size ($P = 1, 3$). This experiment was conducted in order to confirm theoretical predictions from Cain *et al.* (1996) that the scale of heterogeneity must be appropriate to the size of the plant's foraging structures in order for the foraging response to be effective.

Fourth, is integration cost dependent? A basic test of the integration system was carried out by varying the integration cost ($\xi_i = 0, 1, 2, 3, 4, 5$). A value of 0 indicates no integration. It was predicted that increasing costs lower the benefits (W_t) of integration.

Fifth, is integration effective or beneficial in temporally variable environments? Integration by turnover rate was tested by varying ξ_i (0, 2, 5) and T (0, 0.05, 0.10). It was predicted that integration would improve clonal performance (W_t) in temporally heterogeneous environments.

Sixth, is physiological integration more beneficial in resource-poor environments? Integration by environmental richness was tested by varying ξ_i (0, 2, 5) and the patch frequencies where each resource has equal frequencies in each treatment ($F_A = F_B = 0.25, 0.5, 0.75$). For this test it was predicted that physiological integration would be less beneficial in richer environments, a prediction that comes from Alpert's (1999) work on *F. chiloensis*.

Finally, how do integration and foraging interact, in a spatially and temporally variable environment? The foraging and integration systems were tested against environments of varying compositions which were defined as follows. An environment with low temporal predictability was defined by T equal to 0.10; high temporal predictability was defined by T equal to 0.01. An environment with a low spatial predictability was defined by no spatial covariance with F_A and F_B at 0.10. An environment with a high spatial predictability was defined as either negative spatial covariance (with F_A and F_B at 0.06) or positive covariance (with F_A and F_B at 0.32). The differences in patch frequencies between the two high spatial predictabilities adjust for the covariance algorithm so that each resource type was found in 10 percent of patches. Two plant traits were defined: foraging (ϕ_p at 0.25

and λ_p at 1) and integrating (ξ_i at 2). The experiment was conducted testing all combinations of temporal predictability (high and low), spatial predictability (high (+), high (-), and low), foraging (on, off), and integrating (on, off), all while maintaining total patch frequency constant so as to remove a potential confounding factor of differential total resource availabilities. For this test it was predicted that the most successful clones would be the foraging integrating clones in an environment with low spatial and temporal variability. Both foraging and integration should follow the patterns from prior results.

Analysis

For each experiment, each set of parameters was run 200 times. The output parameters (Table 2.3) were collected from each run and were used to calculate several additional statistics. The first, total genet fitness, W_g , was calculated using the following formula:

$$W_g = W_i + N_g \cdot \xi_r \quad (2.2)$$

W_g represents the lifetime fitness pool of the clone, which has been adjusted to include the fitness already invested in making ramets. Successful clones should not be penalized for making many ramets. The second parameter, the morphology index (M), was calculated as follows:

$$M = \frac{m}{N_g} \quad (2.3)$$

It is a measure of the relative frequency of external ramets. As the morphology index approaches zero the clone is more guerilla; as it approaches 1 it is more phalanx in its morphology. The third parameter was an index of dispersal of the genet (D_g), calculated according to equation (2.4):

$$D_g = p_m \cdot l \quad (2.4)$$

It is an absolute measure, in hexagonal units, of the maximal spread from the mother ramet. The last calculated parameter was a measure of coverage (C_g):

$$C_g = \frac{N_g}{W^2} \quad (2.5)$$

It measures the percentage of ground cover. As it approaches 1, the reliability of some other parameters such as the total number of ramets becomes less reliable, as the clone can become space-limited. These calculated parameters are summarized in Table 2.3.

Table 2.3 Calculated output parameters used in analysis of IntegraClone data. Please see text for details.

Parameter	Description	Units
W_g	Total genet fitness pool, including ramet investment	fitness points
M	Morphology index	none
D_g	Dispersal index	hexagons
C_g	Groundcover of clone	none

For these four calculated output parameters, plus the foraging success rate (s) and the mean number of children per node (b), means and coefficients of variation were calculated. The direction and magnitude of differences in the mean outcomes from different parameter sets was noted, but no specific hypothesis testing was used to assess statistical significance. Due to the nature of simulation data, any amount of data could in principle be collected in order to have a sample large enough to show statistical difference between any two numbers. The purpose of the simulation was not to show statistical difference, but rather to show biological significance. Two hundred runs were used for each set of parameters to be sure that a true mean was collected. The means, standard errors of the means, and coefficients of variation for all output parameters were calculated using StatView 5.0 from the SAS Institute.

Literature Review

Search

Before beginning the search, a list of desired data was assembled which included the responses of internodes to varying light and nutrient availabilities, clonal growth parameters collected in the field (internode length, branch frequency, and branch angle), physiological integration studies for various nutrients, as well as life history and biome information.

A bibliography crawl was conducted starting with three papers by de Kroon and Hutchings (1995), Sutherland and Stillman (1988), and Pitelka and Ashmun (1985). These were chosen due to pre-existing review components, allowing the quick accrual of a wide bibliographic base. The bibliography search was conducted chronologically both backwards and forwards in order to reach all existing material on the subject. Additionally, certain key phrases such as “clonal integration,” “clonal growth,” and “physiological integration” were searched for in the Science Citation Index between 1995 and 1999 using the Web of Science (<http://wos.isiglobalnet.com>). Any relevant hits were used as the starting points for additional bibliographic searches.

Any papers providing one of the aforementioned data for a clonal species were accepted as part of the search, and their data included in the review table. For internode length responses to light and nutrients, studies were only used when they statistically tested the response of the plant to a change in resource supply (e.g. Dong 1995). The datum was recorded as positive (+), negative (-), or zero (0) change in internode length in response to an *increasing* nutrient supply. Only statistically significant differences between the study's treatment groups at the $p =$

0.05 level were recorded; results of no difference were coded as 0. Data for shading were split into selective shading, which mimics biotic shading effects with a reduced red to far red ratio, and non-selective shading, with no specified light compositional change. Nutrient response data were separated by nutrient or mineral type.

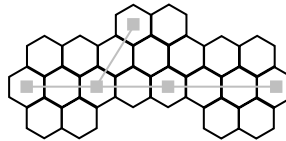
Clonal growth parameters were only recorded for values estimated from field data. Unfortunately such data are rare; collecting a spatially explicit dataset on a reasonably-sized clone is very difficult and time consuming. Mean values are reported in the review table for each population or study

Physiological integration data came from two types of sources: either labelled tracer studies, such as acid fuschin dye and carbon-14 studies, or clonal fragmentation experiments. The former are fairly self-explanatory (see the work of Jónsdóttir and Callaghan 1989, 1990 for examples). The latter are usually conducted with at least two treatment groups. In both cases a mother and daughter ramet are used, and the mother is provided with a particular nutrient, such as nitrogen in the form of a fertilizer. In one treatment group the connection is severed, allowing the effect of integration to become apparent in the non-severed group (e.g. Alpert 1991). The nutrient in question and the direction of transport (if determined in the study) are reported. Note that not all studies tested for both acropetal and basipetal transport; the results of all studies, even if incomplete, are reported. A nutrient's physiological integration is listed as "facultative" only if the study presented evidence that nutrient sharing was not obligate, or if it was shown that the plants were able to allocate resources to specific areas in response to external stimuli such as defoliation.

Life history data were collected from various floræ covering an area to which the species is native. Hydric ecological preferences were noted when those were pronounced.

Analysis

The data were summarized and pooled categorically, using output from StatView 5.0 (SAS Institute). StatView was also used to create frequency distributions for clonal growth parameters (α , ϕ , λ , Figure 1.1). Clonal characteristics such as facultative integration and the presence of a foraging response were tested against life history characteristics of the species to check for independence from biome and hydric requirements, as well as for family or clonal method (stolon vs. rhizome). All Chi-squared tests (χ^2) were performed using Excel 98 (Microsoft) for Macintosh.



RESULTS

“A single line is rarely the shortest distance between three (or more) points; branching and efficiency go hand in hand in the control of space.”
— Adrian D. Bell (1986)

Simulation

A typical output for a run of 30 time steps is shown in Figure 3.1. A copy of the simulation is available on the accompanying CD.

General Notes

Throughout the text that follows, all final fitness values (W_t and W_g) are standardized by dividing them by 1×10^{10} . This was done in order to place them within the same numerical range (0-100, generally speaking) as the other output parameters. The discussion below will show some results in graphical form; full tables with all numerical output appear in appendix B. All graphs of simulation results omit standard error bars due to their generally minuscule size. The standard errors are reported in appendix B.

Repeatability Analysis

A randomly chosen set of parameters was used in a repeatability analysis. After 200 simulation runs the highly variable output parameters (with coefficients of variation routinely above 20) such as total fitness converged on a stable mean (Figure 3.2). “Highly variable” was defined by coefficients of variation routinely above 20.

Figure 3.1 (following page) Typical output for a single run of the IntegraClone simulation program. This output results from a high plasticity clone in an environment with a single resource (dark hexagons) with patch size 3, run for 30 time steps in a world of size 50.

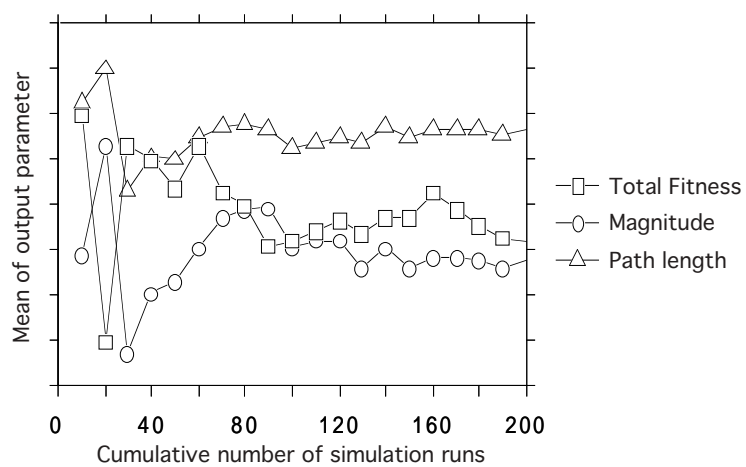
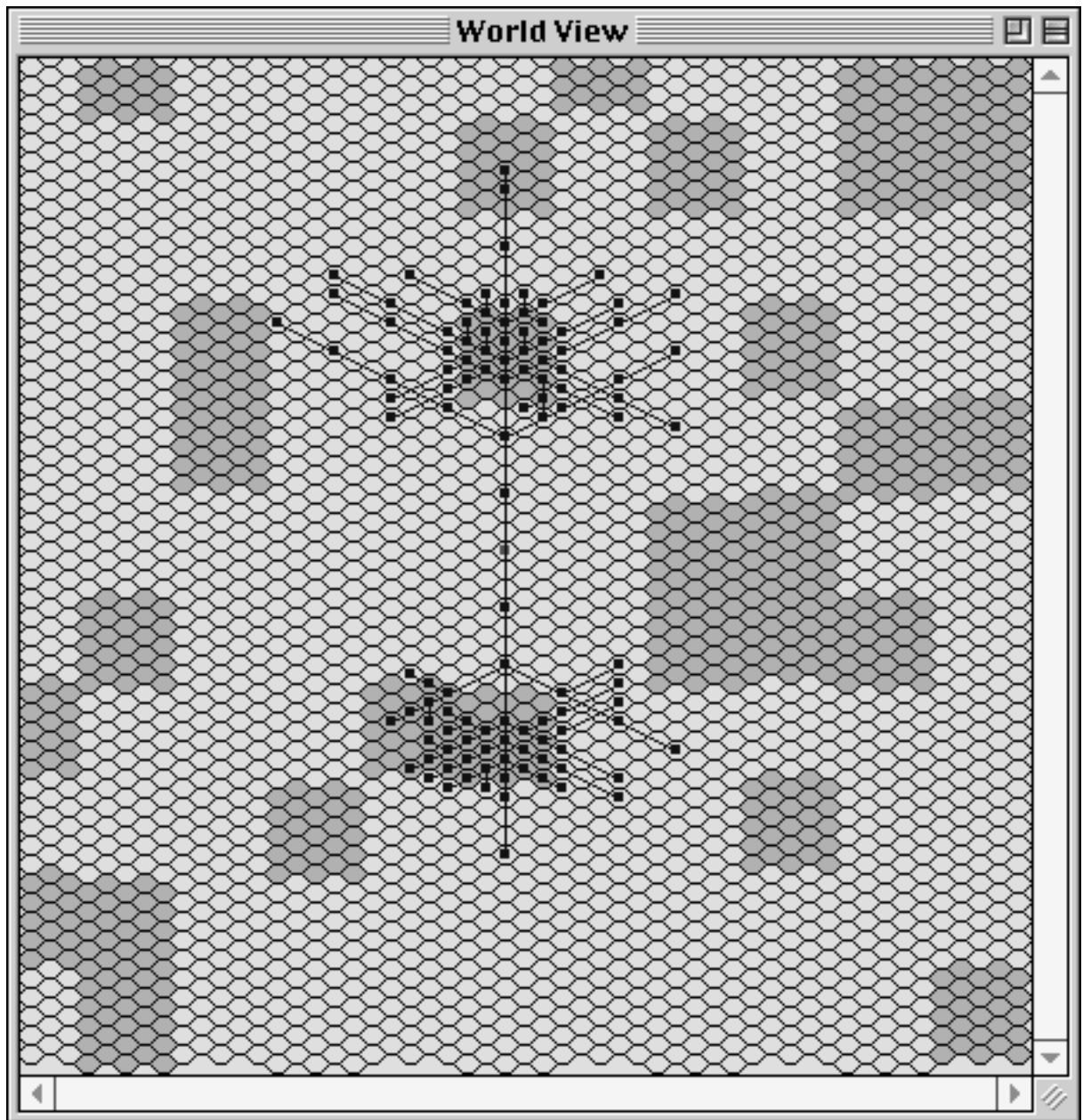


Figure 3.2 Repeatability analysis for 200 simulation runs for three output parameters. The graph shows the mean parameter value for a cumulative random subsampling of the final data for a given parameter set. The total fitness (W_s) is the most variable output parameter in the simulation. Other parameters are not shown due to extremely small variation between simulation runs.

Normality of Output Parameters

A normal distribution comparison was conducted for a randomly chosen run's $W_{g'}$ as seen in Figure 3.3. It proved to be highly normal ($\chi^2 = 0.05$, $d.f. = 2$, $p = 0.975$). Other runs were visually spot checked to be sure all results were normal.

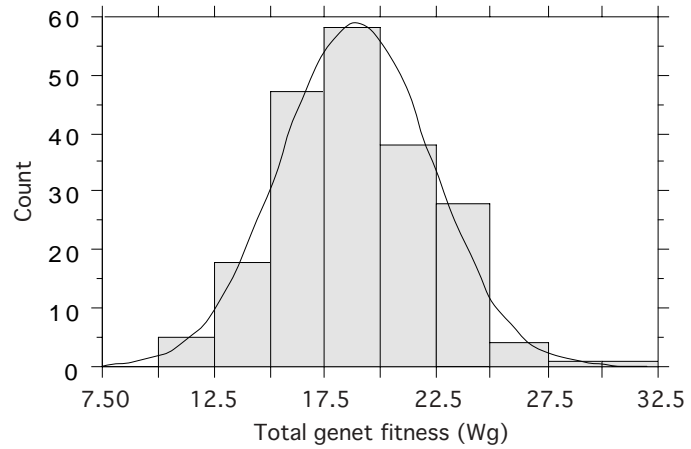


Figure 3.3 Normal distribution comparison for $W_{g'}$, the most variable parameter used as output, for 200 runs.

Plasticity Test

The predictions with respect to foraging success were realized, but the overall fitness (W_g) showed an unpredicted response (Figure 3.4). Clones with the highest foraging success rate had both branch frequency and internode length plasticities, with λ_p and ϕ_p equal to 0.5 and 1, respectively. Branch frequency plasticity was more successful overall with higher success rates and a tenfold difference in $W_{g'}$ even when unaccompanied by internode length plasticity. The coefficient of variation of W_g increased with internode length plasticity, but decreased with branch

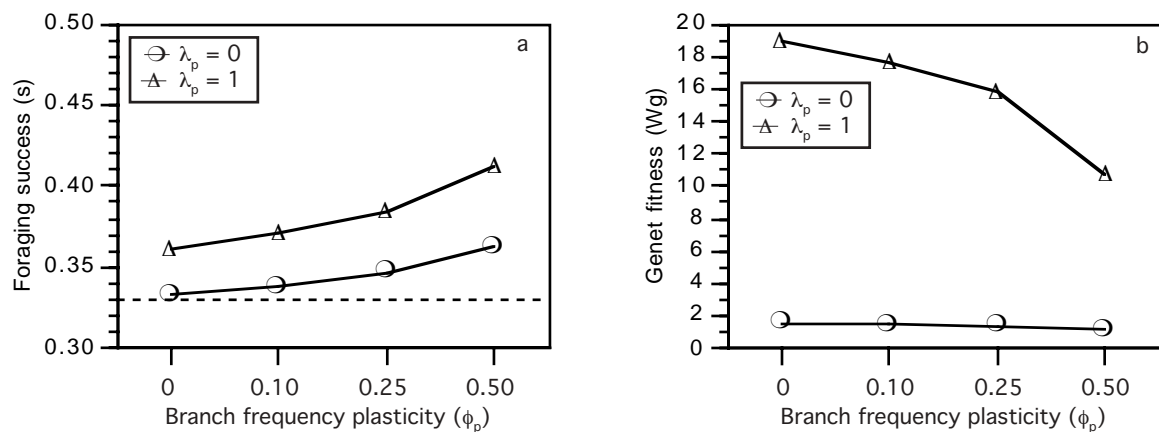


Figure 3.4 Results from the simulation test of plasticity with respect to foraging success rate (a) and total genet fitness (b). The parameters ϕ_p and λ_p represent branching frequency plasticity and internode length plasticity, respectively. Values shown are means of 200 runs.

frequency plasticity. As branch frequency plasticity increased, clones had fewer children per node, less overall fitness, a more guerilla morphology, lower dispersal, and had a smaller number of ramets (less ground cover). Increasing internode plasticity led to more children per node, a more phalanx morphology, longer dispersal, and a much higher number of ramets.

Plasticity by Patch Size Test

All predictions were realized. The most effective foraging strategy was again plasticity of branch frequency and internode length, when employed in large patches (Figure 3.5). Foraging responses were more effective in larger patches, and in small patch-size runs the success rate was no better than random. In some cases it was worse ($\phi_p = 0, \lambda_p = 0, P = 1$; $\phi_p = 0.25, \lambda_p = 1, P = 1$). Decreasing the patch size also led to a higher number of children per node, a decreased total fitness, a more phalanx morphology, a shorter dispersal, and a slightly lowered ground cover. Oddly enough, when the internode lengths were plastic and the patch size was 1, regardless of branch frequency plasticity, absolutely no variation between runs in the success rate was found.

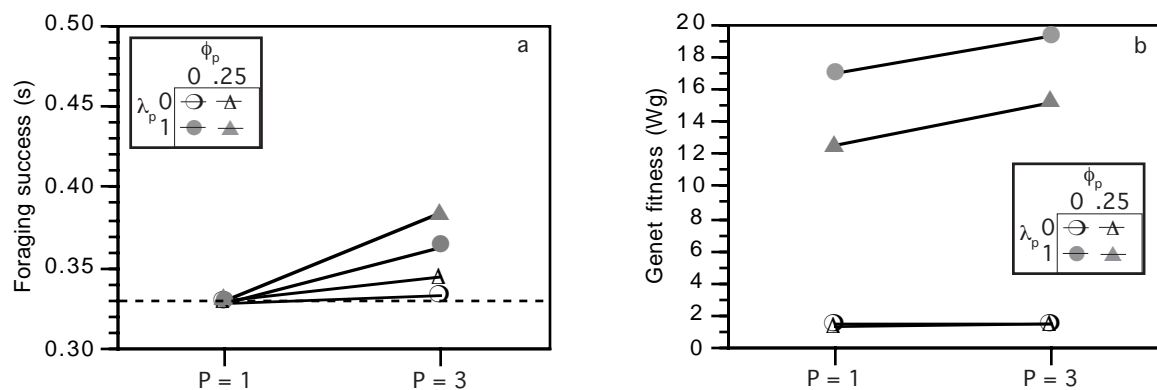


Figure 3.5 Results from the simulation test of plasticity against patch size with respect to foraging success rate (a), and total genet fitness (b). In (a), the dotted line indicates random foraging. The parameters ϕ_p , λ_p , and P represent branching frequency plasticity, internode length plasticity, and patch size, respectively. Values shown are means of 200 runs.

Plasticity by Turnover Rate Test

Predictions regarding the effects of high turnover rates on foraging success were realized. The most successful foraging strategy was plasticity of internode lengths and branching frequencies, in an environment with low temporal variability (Figure 3.6). The higher foraging success rates in the temporally variable environments was due to an artifact of the simulation; the patch turnover algorithm failed to take into account input patch frequencies, and tended to bring the environment to a realized patch frequency of 0.5. In the environments with a patch turnover that was greater than zero, a foraging success rate of 0.5 was no better than random growth. Therefore in this experiment, temporal variability produced no differences between foraging strategies, which were all equivalent to a random non-foraging search. Increasing the turnover rate increased the overall fitness by a factor of 2 to 3, which was in part due to a higher number of ramets. The morphology under high turnover conditions became more phalanx.

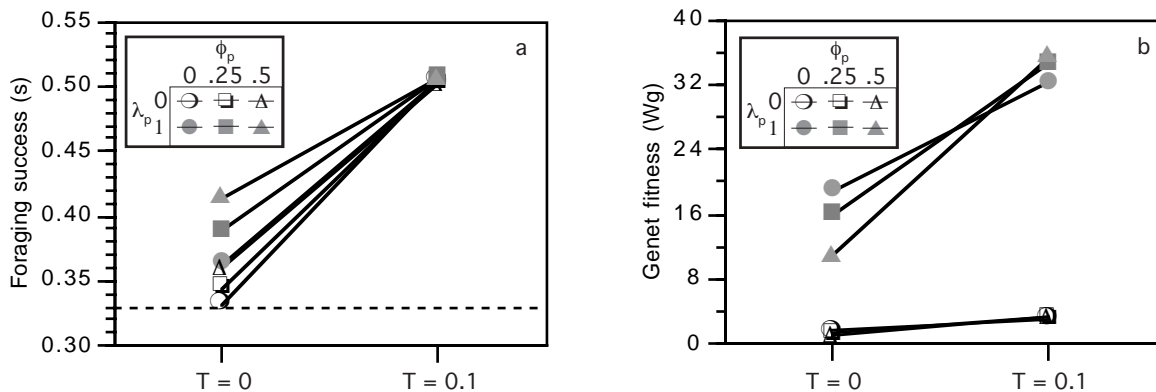


Figure 3.6 Results from the simulation test of plasticity by patch turnover with respect to foraging success rate (a), and total genet fitness (b). The parameters ϕ_p , λ_p and T represent branch frequency plasticity, internode length plasticity, and patch turnover rate respectively. Values shown are means of 200 runs.

Integration Test

Predictions regarding the cost of integration were realized. The most successful strategy in this case was to integrate, with as small a cost as possible (Figure 3.7). Integrating with ξ_m set at two appeared to be less beneficial in terms of fitness than not integrating in this environment, even though integrating with ξ_m set at two or three gave a net benefit in ramet number over the no-integration strategy. No significant changes in clone morphology occurred, except in the case of integration with ξ_m set at 1, where the clone dispersed much further than the other strategies due to its increased number of ramets.

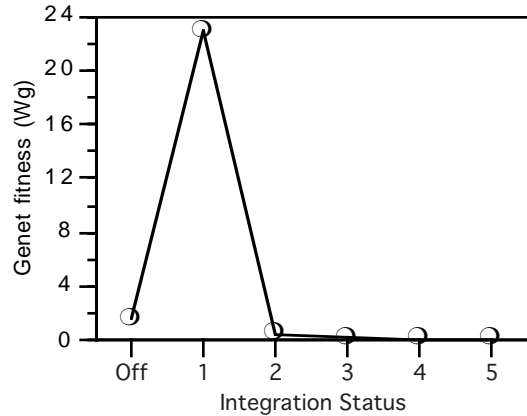


Figure 3.7 Results from the simulation test of integration with respect to total genet fitness. The integration status is either off, or the cost of integration ξ_i . Error bars indicate standard error. Values shown are means of 200 runs.

Integration by Patch Turnover Test

Predictions regarding the benefits of physiological integration in stable and unstable environments were realized. The foraging success again went to 0.5 in environments with patch turnover (Figure 3.8). In terms of overall success, the

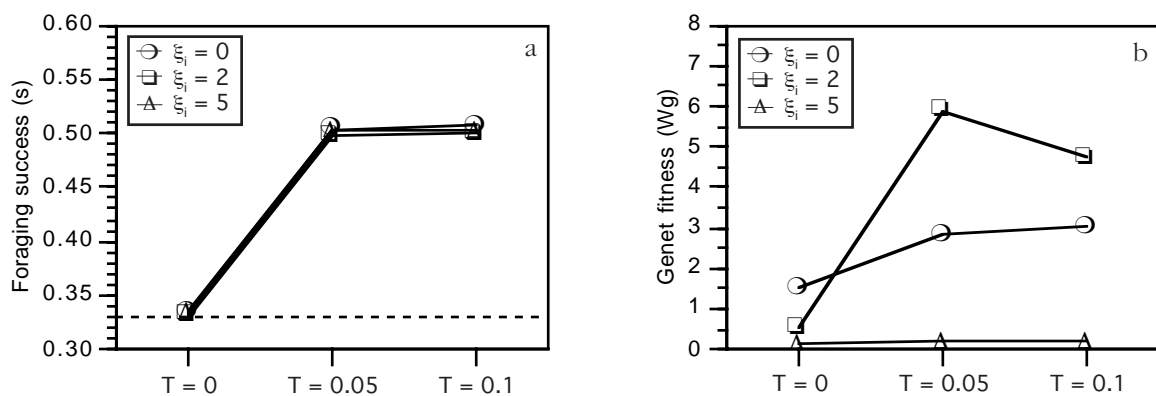


Figure 3.8 Results from the simulation test of integration against patch turnover rate with respect to foraging success rate (a) and total genet fitness (b). The parameters T and ξ_i represent patch turnover rate and integration cost, respectively. Where ξ_i is zero, there is no integration. Values shown are means of 200 runs.

strategy with the most fitness was the integrating clone with the lowest costs in high patch turnover rates. When the overall fitness increased beyond 3, it became hyper-variable, and up to a tenfold increase in the coefficient of variation was seen. With no integration, a highly variable environment produced the highest W_g . No morphological changes were seen, apart from a higher dispersal correlated with both fitness and groundcover, due to the increased number of ramets.

Integration by Environmental Richness Test

Predictions regarding the benefits of physiological integration in rich environments were not realized. The most successful clone in terms of fitness was the one which was integrating with the lowest costs ($\xi_m = 2$) in the richest environment ($F_A, F_B = 0.75$, Figure 3.9). Increasing the environmental richness increased success rates, as well as promoting a more phalanx conformation, longer dispersal distances and more groundcover. The latter two were due to an increase in ramet number, which can be attributed to the

increased resource availability in the environment. One oddity should be pointed out, however; the highly successful clones could not entirely attribute their success to a large increase in ramet number.

Foraging and Integration by Environmental Predictability Test

Predictions were not upheld for this test. The clones with the highest foraging success rate were the plastic clones in the positively spatially predictable environment, closely followed by those in the low spatial predictability environment (Fig-

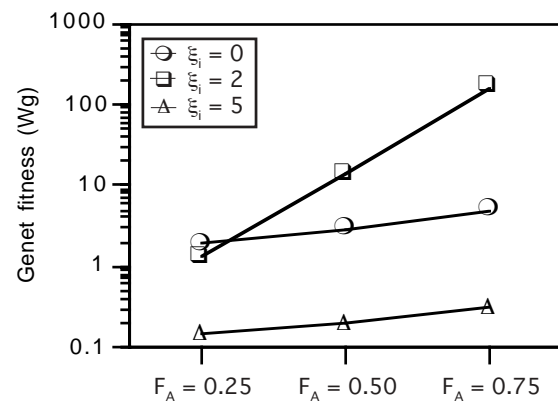


Figure 3.9 Results from the simulation test of integration against environmental richness with respect to total genet fitness. The parameters F_A and ξ_i represent patch frequency and integration cost, respectively. Where ξ_i is zero, there is no integration. Values shown are means of 200 runs.

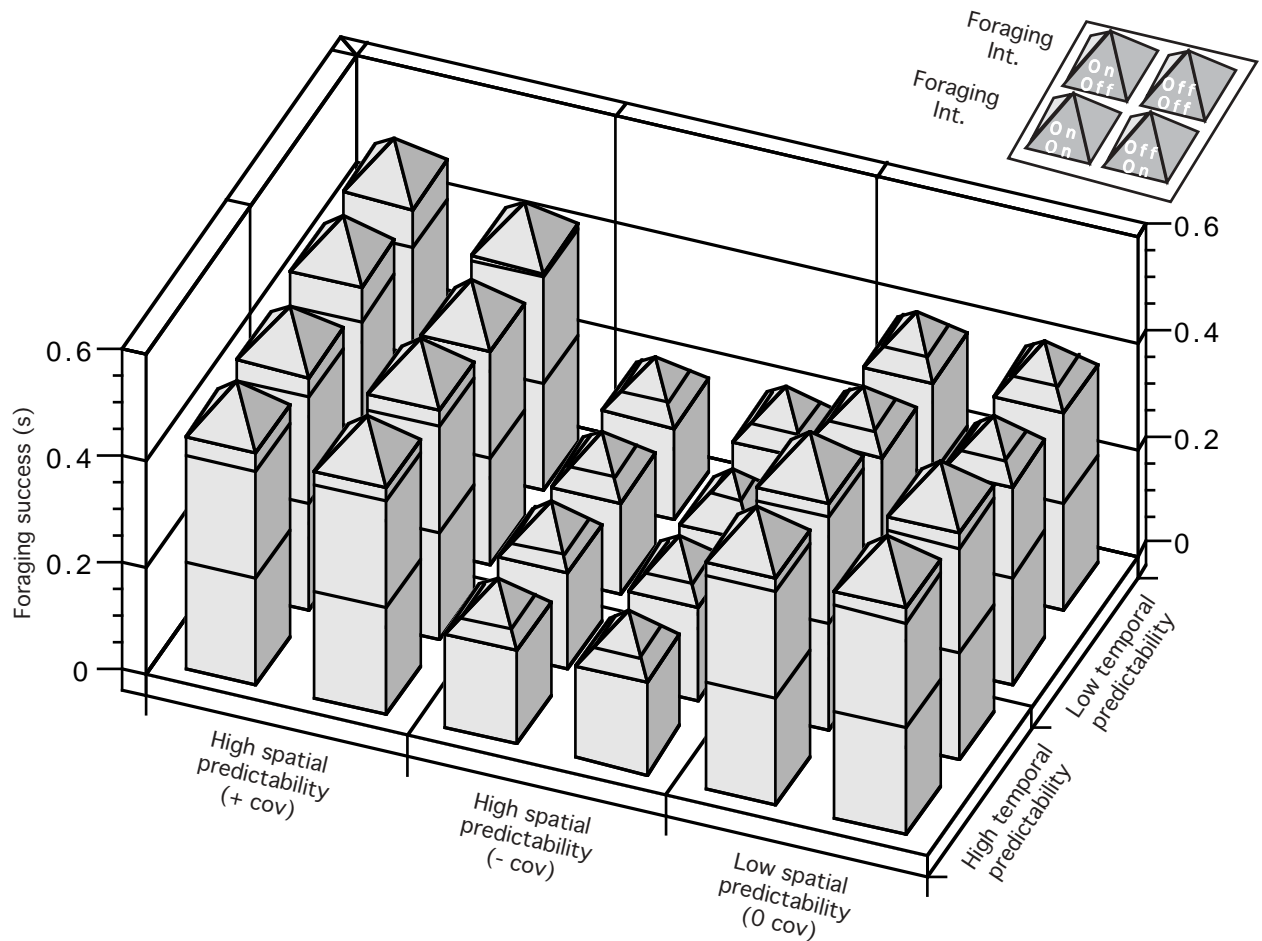


Figure 3.10 Results from the simulation test of foraging and integration against spatial and temporal predictability with respect to foraging success rate. The legend at the top right indicates the values of T , patch turnover rate, and integration status for each obelisk. Please see methods chapter for details of simulation parameter values. Output values shown are means of 200 runs.

ure 3.10). Temporal unpredictability decreased the efficiency of clonal foraging, once adjustments are made for the turnover algorithm bug. The strategy by environment combination that accumulated the greatest fitness was the foraging, integrating clone in a spatially predictable (+) environment with high temporal predictability (Figure 3.11). It was closely followed by the same clone in a similar environment with low temporal predictability, indicating the benefits of integration in a temporally variable environment. The third best combination had a total fitness smaller by a factor of 5, and interestingly enough was a non-foraging, but integrating clone in an environment with high spatial predictability (+) and low temporal predictability.

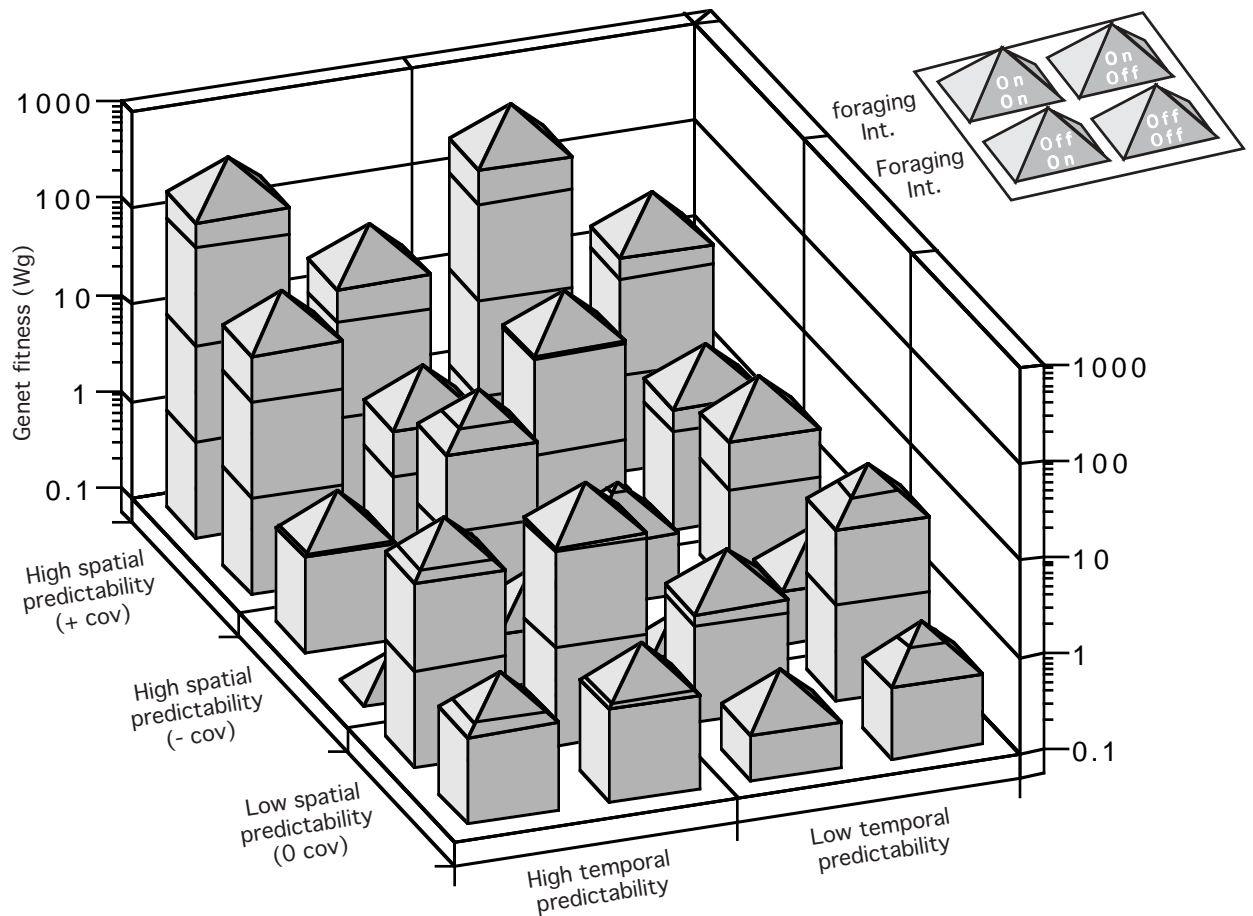


Figure 3.11 Results from the simulation test of foraging and integration against spatial and temporal predictability with respect to total genet fitness. The legend at the top right indicates the values of T , patch turnover, and the integration status for each block of obelisks. Horizontal stripes on the obelisks indicate logarithmic gridlines. Please see methods chapter for details of simulation parameter values. Output values shown are means of 200 runs.

Certain overall patterns were apparent in the data. A high spatial predictability was only beneficial if patches were positively correlated; that benefit in the best case accrued over 500-fold. Foragers generally performed better in spatially and temporally predictable environments, although they performed well in spatially unpredictable environments as well. Integration was only beneficial in spatially predictable (+) environments, but not in (-) environments.

Literature Review

General findings

Data were found for 73 species representing 50 genera in 23 families, including some non-Angiospermae; they appear in full in appendix A. The species come from ecological conditions as diverse as beaches, bogs, and tropical canopies. In all cases except for one tropical liana and two pseudoannuals, the species were herbaceous perennials. For no single species were data found that matched the entire set of sought-after parameters. The best-characterized system, *G. hederacea*, was missing field-based clonal growth data. Data were fairly complete for physiological integration parameters, but rather scarce for field-measured growth parameters. The difficulty of undertaking such studies is most likely to blame (but see Remphrey *et al.* 1982, Klimeš 1992, Kron and Stewart 1994, Piqueras and Klimeš 1998 for excellent examples).

Foraging response

Of the species for which data were available, 33% ($n = 33$) showed a foraging response (decreased λ and increased ϕ in good patches) for non-selective shade, selective shade, or nutrients (Table 3.1). The probability of observing a foraging response was independent of the resource type ($\chi^2 = 2.1$, $d.f. = 2$, $p = 0.35$). More species showed a foraging response for internode lengths than for branching

Table 3.1 Reported foraging responses, broken down by resource, individual component of the response, species water requirements, and clonal method. A foraging response is defined as a decrease in internode length (λ) and an increase in branching angle (ϕ) as resource levels (light, nutrients) increase.

	Foraging	No foraging	Total (n)
Light, non-selective	44%	56%	16
Light, selective	29	71	7
Nutrients	18	82	22
Total	29	71	45
Internode length	34	66	56
Branching frequency	82	18	49
Total	56	44	105
Mesic	32	68	19
Xeric	38	62	8
No water requirements	33	67	6
Total	33	67	33
Stoloniferous	62	38	13
Rhizomatous	15	85	20
Total	33	67	33

frequencies ($\chi^2 = 10.6$, $d.f. = 1$, $p = 0.005$). Of the species for which morphology studies examined multiple resources, 36% ($n = 11$) showed inconsistency in their foraging response, with a discrepancy being reported between different resources.

The probability of observing a foraging response was independent of facultative integration ($\chi^2 = 0.005$, $d.f. = 1$, $p = 0.95$). It was dependent on clonal growth method, however, with a higher rate of foraging in stoloniferous rather than rhizomatous species ($\chi^2 = 7.7$, $d.f. = 1$, $p = 0.006$). When broken down by resource and parameter, selective light showed a distinct bias towards affecting the branching frequency of stoloniferous plants ($\chi^2 = 6.0$, $d.f. = 1$, $p = 0.05$), but no other resource/parameter combinations showed bias. The foraging species were evenly distributed across families ($\chi^2 = 6.8$, $d.f. = 5$, $p = 0.23$), and across biomes for which data were available ($\chi^2 = 3.7$, $d.f. = 5$, $p = 0.59$).

Clonal Growth Parameters

As mentioned above, few data were available on clonal growth parameters, and little analysis was possible due to this paucity of data. Six out of 16 species for which internode length data were available showed average internode lengths between 2.5 and 5 cm (Figure 3.12). The branching frequency data showed a bimodality that is very suggestive (Figure 3.13). The branch-

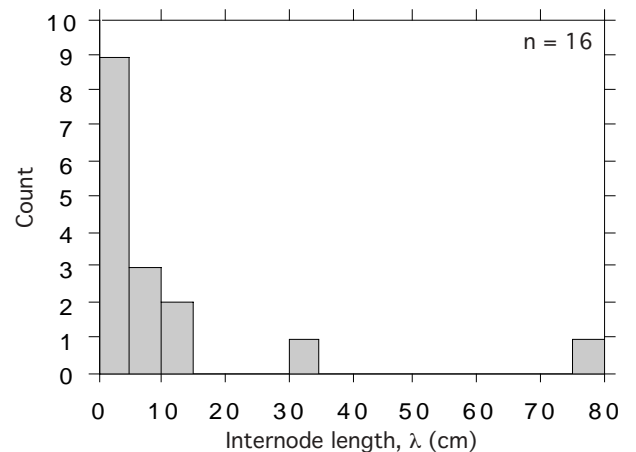


Figure 3.12 Distribution of clonal internode lengths reported from the literature.

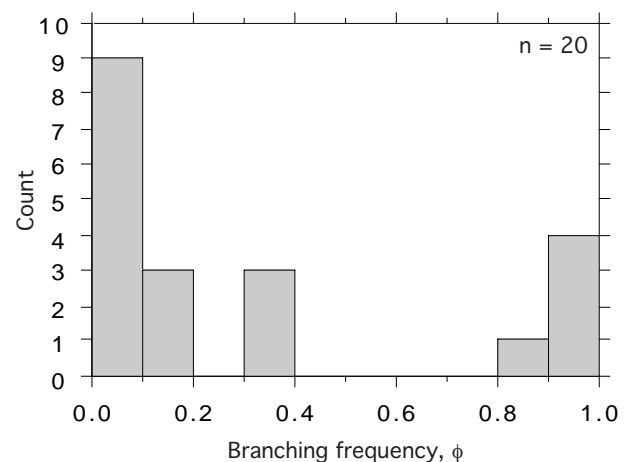


Figure 3.13 Distribution of clonal branching frequencies reported from the literature. Note the bimodality.

ing angle data suggest a uniform distribution (Figure 3.14), but too few data are available for statistical testing.

Physiological Integration

In some cases it was impossible to tell from the published report the direction in which integration occurred. Facultative integration was found to be independent of

clonal method ($\chi^2 = 2.0$, $d.f. = 1$, $p = 0.15$; Table 3.2) and from biome ($\chi^2 = 3.2$, $d.f. = 6$, $p = 0.78$). No single resource showed an excess of facultative integration ($\chi^2 = 3.3$, $d.f. = 2$, $p = 0.36$; Table 3.3). Both reported cases of facultative water sharing come from plants in xeric environments. Carbon sharing was evenly distributed across environments ($\chi^2 = 2.2$, $d.f. = 4$, $p = 0.90$), as was nitrogen sharing ($\chi^2 = 3.9$, $d.f. = 6$, $p = 0.69$).

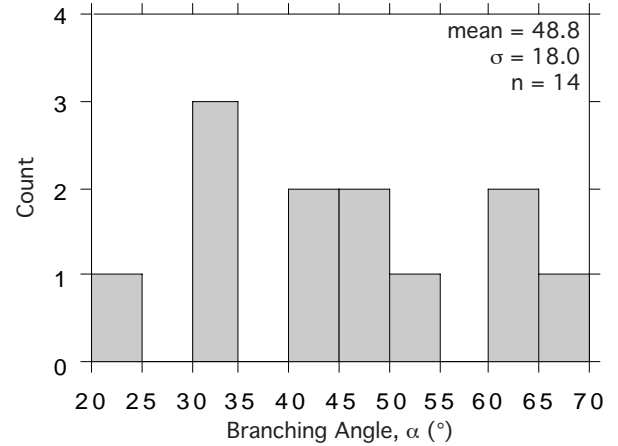


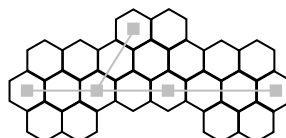
Figure 3.14 Distribution of clonal branching angles reported from the literature.

Table 3.2 Reported facultative integration, broken down by clonal method. Facultative integration of any resource is counted as “Present.”

Facultative Integration	Present	Absent	Total (n)
Stoloniferous	8%	92%	12
Rhizomatous	29	71	24
Total	22	78	38

Table 3.3 Physiological integration between ramets for given nutrients as reported, broken down by direction of transport. The reported studies used either tracer or severing methods. A indicates acropetal transport, B indicates basipetal, (B) indicates only a little basipetal transport, and U indicates the direction is unknown; F indicates facultative transport.

Direction	Carbon	Water	Nitrogen	Phosphorus	Total
A	3.1%	20.0%	42.9%	25.0%	16.9%
B	12.5				6.2
A (B)	12.5	6.7	14.3		10.8
A/B	25.0	53.3	28.6	75.0	35.4
A/B (F)	31.3	13.3	7.1		20.0
U	15.6	6.7	7.1		10.8
Total (n)	32	15	14	4	65



DISCUSSION

“First question: do animals and plants as living bodies become confused with one another at some common point in the series which they form? Or is there some trenchant and exclusive character that sharply separates the former from the latter?”
— Jean-Baptiste de Lamarck

To my knowledge, this is the first study to model physiological integration in a growing clone and investigate its benefits in a spatially and temporally heterogeneous environment. My results indicate that physiological integration can help clonal plants in a temporally heterogeneous environment by allowing them to distribute resources between ramets and also by providing a benefit to the genet as a whole by minimizing intraclonal competition.

Foraging Responses

The simulation foraging test predicts that a full foraging response is most advantageous in locating good patches, but that of the two plasticity factors involved, the internode length plasticity is clearly the most beneficial feature to change in terms of overall fitness. A close examination of the data from the literature review reveals that an appropriate foraging response was found in more species for internode length than for branching frequency, confirming the prediction of the model. The internode length plasticity might be more prevalent due to certain morphological constraints, such as pre-determined meristem location and number (Salzman 1985), which limit the amount of branch frequency plasticity *before* the ramet can process information from its immediate environment. This result also mirrors prior simulation results (Oborny 1994a). From a theoretical standpoint it might be more beneficial due to the cost of intraclonal competition (Cook 1985, Oborny 1994b).

A true foraging response that combines both plasticity factors (internode length and branching frequency) must be evolutionarily beneficial, as a third of the species surveyed displayed one in the greenhouse. The simulation makes such a prediction. In my survey results, a foraging response is correlated with difficult ecological conditions such as extreme water regimes, confirming the hypothesis that foraging allows plants to find good patches in demanding environments (Sutherland 1987). The next expectation is that foraging responses would be correlated with extreme biomes, but insufficient data are available to test this prediction.

The observed correlation between foraging and the stoloniferous habit may simply be due to the speed and ease of such studies. Rhizomatous species generally have a much slower growth.

Scale of environmental heterogeneity

There is a long-standing theorem in heterogeneity theory: the degree of observed heterogeneity is scale-dependent (Allen and Hoekstra 1991). The effectiveness of the foraging response is predicated on the perception of patches by the plant — which is based on the scale of morphology of the plant itself (Hutchings 1999). There are some experimental data to back the prediction that the foraging response is tied to the perception of patch size (Wijesinghe and Hutchings 1997). My simulation firmly supports the theory and predicts the observed empirical result. This implies that clonal plants should prove useful as phytometers of environmental heterogeneity, responding at a scale that is appropriate to their native habitat. For example, based on the guerilla growth form of *F. chiloensis*, the simulation would predict that the patches in the beach strawberry's environment are few, and far between (i.e., gap sizes are large). As predicted, the beach environment follows this pattern (Alpert and Mooney 1996). This result could potentially be-

come a very useful tool to biologists interested in investigating resource availability in certain environments by using plants as the instruments to measure heterogeneity.

The argument of scale-dependent heterogeneity also applies in the temporal dimension. My simulation predicts that plastic foraging is only effective in temporally predictable environments, which mimics the simulation results of Oborny (1994b). The growth rate of *F. chilensis* would therefore suggest a low temporal variability. Evans (1989) performed a temporal variability analysis of resources on an eastern american beach, and found a high degree of change on a daily basis (with the tides), but a low amount of variability over a two month period. A clone's architecture cannot respond to daily events, but it certainly responds to events that take place at a larger timescale. The model predicts this kind of variability in the temporal axis for *F. chilensis*. A high amount of temporal variability ($T \sim 1.0\%$) would lead to a more phalanx morphology than is seen. Charnov's MVT (1976) predicts that a sit-and-wait foraging strategy is more beneficial when prey move a lot. The plant's prey, nutrient patches, if volatile, would lead to a sit-and-wait strategy, a result found by my simulation.

Clonal costs

One puzzling result from the plasticity test needs explanation. The most successful foraging strategy also had a comparatively low fitness. In fact, given a λ_p of 1, increasing ϕ_p from 0 to 0.5 increased the success rate while decreasing W_g . Why would branch frequency plasticity lead to a reduced fitness? The most successful strategy also had the smallest number of ramets, as indicated by C_g . In zones where clones are proliferating, intra-clonal competition for space prevents ramets from reproducing, which would lead to a reduced number of ramets. Unhindered growth gives an exponential increase in ramets, and an exponential increase in the intake

of resources. Hindering that growth reduces the overall success of the clone. This backs predictions made by Cook (1985) and others (Oborny 1994b) regarding intracolonial competition.

Physiological Integration

Averaging out the environment

At low costs, integration provided benefits in multiple ways. The primary benefit confirms the theoretical hypothesis that integration allows clones to overcome temporal heterogeneity (Salzman and Parker 1985, Schmid and Bazzaz 1987), as shown by the environmental predictability test. In environments that were unpredictable, integrating clones accumulated more fitness than non-integrating clones. Second, integration allowed clones in environments with negatively covarying resources to have ramets complement each other. Third, integration allowed ramets in good patches to supplement the fitness intake of ramets in patches that were not as rich. Lastly, although this is a corollary to the third benefit, integration redistributed resources from the inside of the clone out to its periphery. With no integration, once an early ramet had all of its possible children (1 if not branching, 3 if branching), all it could do was collect fitness and store it. That fitness adds to the genet's overall fitness at a constant rate determined by the patch value of the ramet. But reinvesting that fitness into the new ramets allowed integrating ramets to reproduce much quicker and make more ramets. These fostered ramets then also collected resources from the environment, increasing the genet's fitness by the initial ramet's intake rate *plus* the intake rates of all fostered ramets.

This process increases the intake rate faster than exponentially — the ramet number growth curve follows a modified Fibonacci series where the *three* previ-

ous terms are added together instead of only two. This faster than exponential increase in fitness intake rates can be seen in the spectacular results of integrating clones in the environmental predictability assay. These results fit the observation that clonal plants support new ramets via internode connections (Jónsdóttir and Watson 1997).

Hartnett and Bazzaz (1985) claim that physiological integration allows the plant to “average out the environment.” This hypothesis implies that ramets would all show the same final growth morphologies due to a consistent internal physiological state. This view is overly simplistic and has been rejected by empiric data (Hutchings and Price 1993). In some sense though, it is true. Hutchings and Price reject the original hypothesis by showing differential plastic responses of ramets of a single integrated clone growing in a patchy environment. What they fail to consider is that the plasticity may be dependent on local resource intake rates, not on internal physiological conditions. The simulation behaved in this manner, with plastic responses gauged to local conditions, and all ramets having the same internal fitness status.

Non-additivity and non-linearity of benefits

The simulation results clearly point to a case where the benefits of physiological integration which are non-additive. A close examination of the foraging clones in environments with a high spatial predictability shows that adding integration provided an eight-fold benefit in temporally variable environments, but a 14-fold benefit in temporally stable environments. This allowed the clones in the temporally stable environments to overcome and even to surpass the temporally variable clones, despite the enriched patch frequency of the temporally variable simulation runs, thereby achieving the highest observed W_g of any input parameter combi-

nation. This points to prior theoretical predictions that certain strategies are optimized for certain environments (Oborny 1994a, b, Cain *et al.* 1996). This result might also aid biologists attempting to use clonal species as phytometric environmental quality indicators.

The potential for non-additive benefits with respect to physiological integration has been pointed out previously. Alpert (1999) presented a similar model for a different level in the hierarchy of clonal plant organization (Figure 4.1). His model is based on the relationship between two different ramets in the same clone which may be sharing resources. He concludes that a non-additive benefit for the integration recipient (Figure 4.1c) is probably the most common situation in nature. Caraco and Kelly (1991)

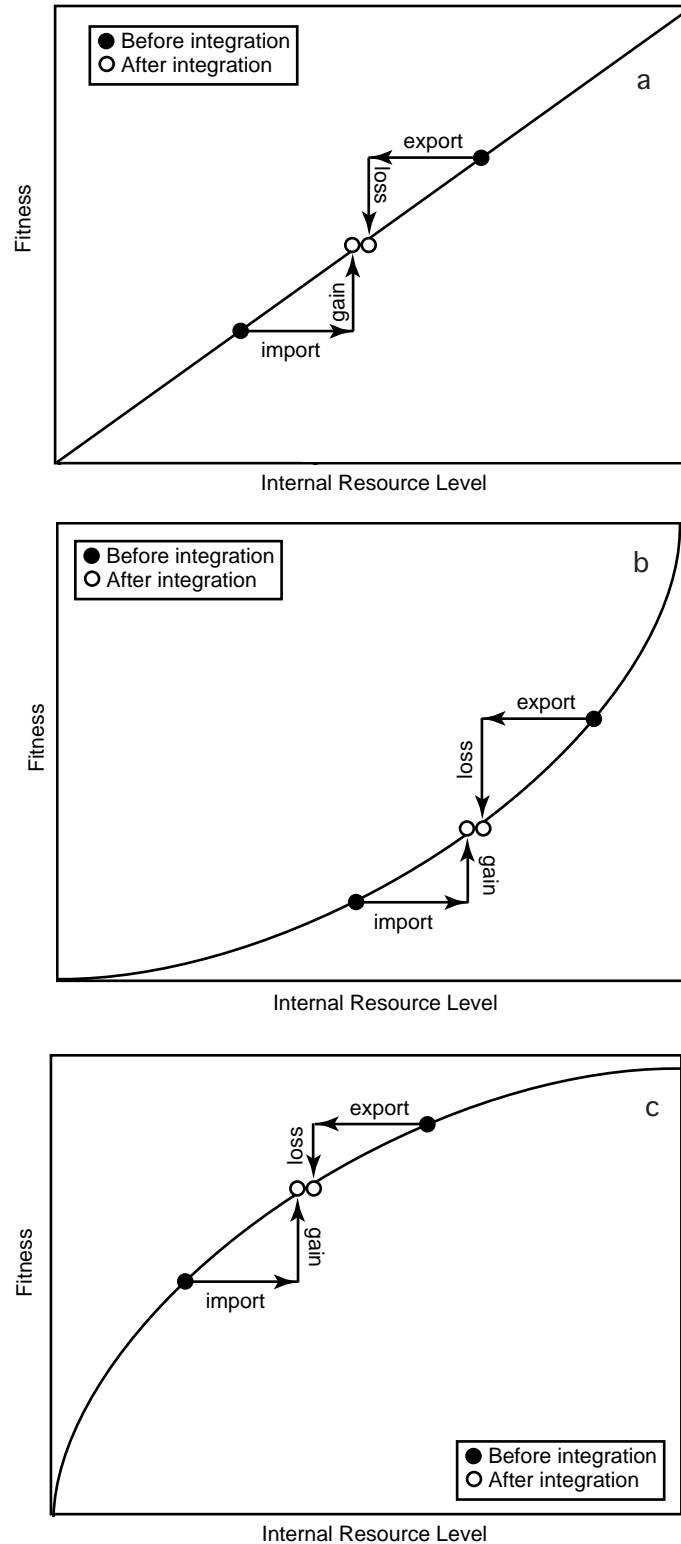


Figure 4.1 Predicted effects of resource sharing between ramets on plant performance in a patchy environment, dependent on the nature of the resource to performance curve: linear (a), convex (b), or concave (c). Sharing should only be advantageous in the case where the curve is concave (c). From Alpert (1999).

mathematically modelled physiological integration between a single mother and a single daughter ramet, and claimed that resource benefit curves are concave (Figure 4.1c). In the case of my simulation, the model used for implementing integration is the one presented in Figure 4.1a, where the net loss of one ramet equals the net benefit of another. This additive model can provide a non-additive benefit one level higher in the organizational hierarchy, which may provide for interesting further theoretical studies which would lend themselves to confirmation by experimentation via cost-benefit analyses of plant resource budgets.

Water

The integration of water presents some especially interesting results that bear on the current discussion. Alpert and Mooney (1986) showed in a fragmentation study of mother-daughter ramet pairs that daughters who were suspended in mid-air and not allowed to root suffered no ill effects if the mother was kept well-watered. Additionally, they showed no cost to the mother at all. Because water is moved passively through cohesion-tension in the xylem, plants have no investment beyond the initial spacer growth to move water between ramets. The entire process is driven by water potential gradients. For the same reason, water may show less directional constraint on transport than other minerals (Marshall 1990). This result suggests that facultative integration would be extremely prevalent for water, even though my literature review failed to detect such a conclusion. This is likely due to the small number of studies that describe facultative water integration. All three of the studies that had the potential to show such a phenomenon found it, though two studies occurred in the same species (Alpert and Money 1986, Evans 1991, Evans and Whitney 1992).

Some of the other resources are postulated to follow the direction of water

flow, due to their mechanism of transport in the xylem. For example, nitrogen has been shown to follow the flow of water in *G. hederacea* (de Kroon *et al.* 1998). This does not remove potential costs from the transport of such minerals, however. They still must be pumped into and out of the plant's xylem at each ramet that is sharing or receiving.

Evolutionary context

Just as clonality is thought to be ancestral in the Angiosperms (van Groenendael *et al.* 1997), integration is thought to be ancestral in clonal plants (Kelly 1995). Its prevalence among clonal species (42% of all species surveyed) indicates that it is likely to have some evolutionary benefit (see also Jónsdóttir and Watson 1997), a prediction supported by my simulation trials. The simulation predicts, however, that integration is most beneficial in environments that are temporally variable. We would therefore expect to find a preponderance of integrating species in highly temporally variable environments, a prediction which is not supported by the literature survey (although a trend is apparent). On the other hand, Jónsdóttir and Watson (1997) after a brief literature review claim that physiological integration is prevalent in resource-poor environments.

The second-order modularity of clonal plants provides an additional point of interest in an evolutionary context. As organisms which have multiple, hierarchical levels of interaction between the genotype and the environ-

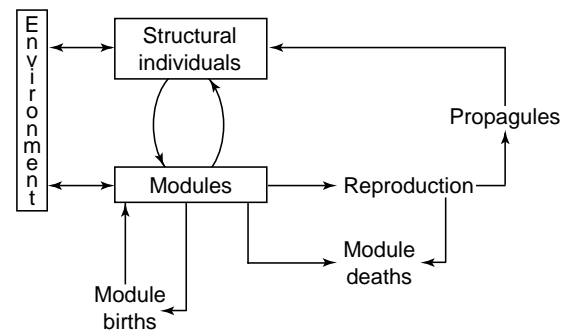


Figure 4.2 Basic processes required for hierarchical phenotypic selection in modular organisms. The fitness of a propagule establishing the structural individual depends on module births and deaths, as well as on average propagule production by modules. These fitness components are influenced by interactions both at the module-level and at the level of the structural individual. From Tuomi and Vuorisalo (1989a).

ment (ramet, genet), they can have selection working at both levels (Figure 4.2, Tuomi and Vuorisalo 1989a). In the case of physiological integration, Alpert's model (1998) of non-additive benefits might be operating at the level of Tuomi and Vuorisalo's module, whereas the non-additive benefit discovered by the simulation model would operate on the structural individual module. Both could be selected for independently. This implies that in certain species one or the other benefit would be evident, but not both. Looking across species should find all combinations. Due to the recency of Alpert's prediction, no empirical integration studies have yet examined this phenomenon.

The simulation treated each clone as a single IPU (integrated physiological unit). This is the extreme case, but there is evidence that clonal species are much more highly integrated than non-clonal herbs (Marshall 1996). These results must therefore be tempered in their application, as clonal plants usually have more than a single IPU, organized around primary stolons or rhizomes (Price *et al.* 1996).

Further simulation studies could be conducted that replace the averaging integration scheme used here with a source-sink model. Such a model would lend itself very easily to defining sectors of integration in a plant; these could be organized as the authors desired (see Kaitaniemi and Honkanen 1996 for an example in a non-clonal species).

Unlike with the foraging tests, the tests of physiological integration have no prior simulation benchmark with which they can be compared. The integration test provides a way to evaluate the usefulness of the results, however. They match up with theoretical predictions regarding benefits and costs of integration (Pitelka and Ashmun 1985, Cook 1985). Given a certain set of environmental conditions,

costs eventually exceeded the benefits and severely reduced the genet's overall fitness.

Literature Review Difficulties

Unfortunately, trends that were sometimes apparent in the data collected from the literature could not be confirmed statistically due to small sample sizes. For example, tests of even distribution across families were doomed to failure; a large number of families only had one species capable of participating in any given analysis, and the rest only had 1 or 2 individuals showing the trait in question. Chi-squared tests are not very powerful detectors of difference in these cases. Two glaring examples stand out. First, better studies on the nature of physiological integration would prove extremely helpful. Many of the studies only tested for flow in a single direction, or only reported qualitatively that integration occurred. Secondly, more field studies of growth patterns with special attention paid to Bell's three growth parameters would be very enlightening, especially when combined with a geostatistical quantification of locally available resources (e.g. Jackson and Caldwell 1993a, b) to allow for a determination of field-observed plastic responses.

Simulation Accuracy

Chosen parameters

One of the parameters chosen for output (or calculation) needs clarification. The morphology index, which is an indicator of phalanx as opposed to guerilla morphology, was chosen as an output because of the ease with which it can be calculated, and its lack of reliance on groundcover. It also overcomes the problem pointed out by Cain (1991, 1994) that a statistically significant change in rhizome or stolon length does not necessarily equal a significant change in genet dispersal.

Several other indices were also considered, but rejected. The Morisita index (Morisita 1959), which is based on the geometric shape that a clone occupies on a map, becomes less reliable in a simulation setting where the plants begin filling the available space, as there are unnatural spatial constraints operating on them. It is also tremendously difficult to calculate algorithmically, although its ease of measurement has led to fairly widespread use in the literature (e.g. Birch and Hutchings 1992). All indices that are based on quadrat analyses suffer from this shortcoming (Goodall and West 1979). Other indices, such as the plastochron index (Erickson and Michelini 1957) can be highly variable within a clone due to plastic responses and can fail to accurately describe the growth form in a highly plastic individual. It describes growth patterns in a temporal manner. The plastochron index has been highly used in the literature (e.g. Birch and Hutchings 1992a, b), but is inappropriate for a simulation study of this nature, as the temporal growth process is rather constant in my simulation and a plastochron would be uninformative.

Quality of results

The simulation accurately reproduced results from Cain *et al.* (1996), Oborny (1994b), and Sutherland and Stillman (1988). My results predict that internode length plasticity is beneficial in locating good patches in the environment, a prediction made by all three prior simulation studies. My results also predict that branching frequency plasticity is beneficial in locating good patches, a prediction made by Oborny (1994b) and Sutherland and Stillman (1988). My simulation also predicts that increasing patch size improves the foraging success rate (plasticity against patch size test), which echoes Cain *et al.* (1996). Finally, my simulation predicts that temporal heterogeneity decreases foraging efficiency, as seen in Oborny (1994b, but see below).

One error was detected in the simulation, which explains the only nonsensical results observed. Specifically, the model predicts that in the absence of plasticity, temporally variable environments improved the foraging efficiency. This is due to an unfortunate oversight in the patch turnover algorithm used for my simulation, which fails to take into account patch frequency inputs. In an environment with a reasonable turnover rate (0.1%), the algorithm tends to bring the patch frequencies to 0.5. Hence the reported increase in success rate—the foraging efficiency for environments that include turnover must use a value for F_A of 0.5 as a benchmark. A corollary to this difficulty is that in experiments that include temporal variability, runs with and without variability cannot be directly compared for foraging success. Clones in the richer environment are also expected to have a higher overall fitness (W_g), since the environment is richer. The previous discussion of the results took this bug into account, and all discussions of foraging efficiencies are apparently correct.

Theoretical choices

Based on the results of Salzman (1985) regarding the developmental patterns of meristems in new ramets, it was decided that all ramets would have their branching fates fixed at birth. Her results were not the only reason, however. To program the model otherwise would entail another set of parameter input decisions based on the method used to determine if a ramet would branch. The most logical decision when considering the biology of clonal plants would be to have ramets branch based on their internal resource state. This would require additional input parameters based on how to choose to branch, as well as what the cutoff level would be. It would also lead to inevitable branching in large clone situations, which is unrealistic.

Experimental choices

Decisions had to be made as to what data to collect. The temptation with simulation experiments such as this one is to collect data on the full range of input values for all parameters, and to generate a multi-dimensional dataset for them. Unfortunately, time and computational constraints make this difficult — not only is collecting the data difficult in such a case, but analyzing it is even more challenging due to the size of the resulting datasets.

The first set of experiments were designed to test the validity of the simulation, and to insure that it was replicating prior results. The tests of plasticity, plasticity by patch size, and plasticity by turnover all fit into this category.

The second set of experiments were designed to test the integration system. The integration and integration by turnover tests were designed to verify that the algorithm worked. The integration by environmental richness test was designed to examine certain empirical results (Alpert 1999) to insure that the algorithm was generating predictions that would be applicable to empirical data. A useful expansion to this set of experiments would be to test integration in a homogeneous environment (or near-homogeneous environment) to ensure that integration provides no benefit under such conditions. All tests should also include a test of integration with a cost of zero.

The last experiment (integration and foraging by environmental predictability) was designed to put together the two main simulation systems, and to test them against a range of environments. Environmental predictability was chosen (both spatial and temporal) in order to generalize the applicability and to prevent testing for one specific biome, such as a beach. The spatially structured environment was run in two different flavors, with positive and negative covariance be-

tween resources, because each type has similar predictability and could occur in nature. Here again integration should be tested with a cost of zero.

The simulation still holds the key to a great deal of answers. For example, instead of fixing a feature of the environment and placing different genotypes in it, the simulation program can be made to operate in reverse. Fix a genotype with certain plasticity and integration traits, and find out which environment it is optimal for. An even more useful set of experiments would be to investigate the relationships between the various cost parameters and the patch values. Such experiments would choose a handful of genotypes (e.g. Oborny 1994b) and try them against various environments for which the costs:patch value ratios are varied.

Reworking Foraging Theory

Comparisons with Animal Foraging

Plant foraging theory grew out of an analogy with animal foraging theories. A genet selectively places its ramets in good patches. Since it is seeking out those good patches through a plastic growth form, the analogy is straightforward. This analogy is missing something, however, which both likens plant foraging to animal theories as well as distances the two. Physiological integration allows the foraging plant to share acquired resources between its ramets just as an animal apporitions its resources between its various organs. In this sense the animal is an obligate integrator. The primary difference is one of time scale: plants simply forage very slowly. But a second difference that is implied is that via their second-order modularity plants can forage in multiple places at once, something which animals (unless clonal and integrated, such as corals) are incapable of doing. This has several interesting implications which will be dealt with below. To my knowledge, no reasonable foraging model exists for such a situation.

Marginal Value Theorem

Since no special foraging model exists, the marginal value theorem (MVT, Charnov 1976) is therefore the theory of choice to describe plant foraging situations. The MVT attempts to maximize the resource intake rate, and only manipulates the travel time between patches (analogous to a plastochron), the search time within a patch (analogous to ramet lifespan), and the intake rate in a patch of a given type. Since it is the simplest foraging model that deals with patchy environments, it can easily be modified (as described above) for plant systems. This has only been done for a single species, *Cuscuta subinclusa* (Kelly 1990).

To date, only Samu (1991) has performed a theoretical comparison between foraging concepts in plants and animals (Samu 1991). He points out several shortcomings of the MVT when applied to botanical situations. For example, in plants certain resources like light cannot be depleted. The MVT is based on the depletion of resources in patches — the equivalent of RDZ's (resource depletion zones). To date, most plant foraging papers have only included data regarding the internodes. This fails to consider costs and benefits associated with feeding structures (i.e. ramets). My simulation fails to include sufficient information in order to calculate a MVT— the effort in a patch, and the net energy gain in a patch are constant, and therefore cannot be optimized. A simulation study could easily be constructed to address these issues, based on the experiments described above regarding costs:patch value ratios.

Economics

One interesting side-note about clonal plants having multiple mouths is found in division of labor theory. This has only recently come to the forefront in the plant foraging literature, being primarily spurred by a good review from Bloom *et al.*

(1985). The prevalence of facultative integration in the species surveyed would seem to indicate that division of labor is an effective technique for clonal plants in allowing them to overcome environmental conditions. Certain cases, such as that of *F. chiloensis*, highlight how division of labor might be especially useful in certain conditions. De Kroon *et al.* (1994) point out that in heterogeneous environments, physiological integration and a division of labor might be more beneficial than a plastic morphology. The simulation results support this prediction: in highly variable environments, foraging provided no benefit, but integration allowed clones to prosper. Adding a division of labor benefit would only enhance the result.

Hamilton's Rule

The other interesting point regarding clonal plants having multiple mouths comes from the animal behavior literature. W.D. Hamilton (1964) proposed a very simple rule regarding the evolution of altruism:

$$R \cdot B > C \tag{4.1}$$

In equation (4.1), B is the benefit to the recipient, C is the cost to the altruist, and R is the coefficient of relatedness, essentially equal to the amount of shared genome between the individuals. Hamilton's rule might have extensive implications for cases like *Ficus* and *Rhinanthus* where genetically distinct individuals show physiological integration. For clonal plants, in any genet R is equal to one, which modifies the equation:

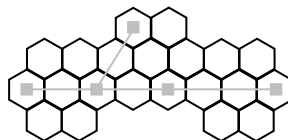
$$B > C \tag{4.2}$$

This theoretical result fully supports Alpert's (1999) model (Figure 4.1), and allows additional comparisons between the plant and animal literatures. For example, social insects such as ants have been extensively studied using this rule, and many

modifications that have been made to it. E.O. Wilson's work on leafcutter ants (1980) might yield some insights into the performance of plant genets in empirical studies.

Summary

Simulation models lend themselves very well to the study of clonal plants. They allow a graphical output that can be interpreted biologically, and can perform time-consuming analyses of clones in a matter of milliseconds. Once the initial investment in programming time has been made, a nearly infinite amount of data can be collected. We have seen how a simulation can be problematic, or successful. Coding errors can occur but those can still be informative, and their nonsensical results can be easily traced. We have seen how a simulation can repeat theoretical predictions, as was seen in the optimality of certain strategies for certain environments. Simulations may also make new theoretical predictions, as was seen for the non-linear benefits of physiological integration in patchy environments. Simulation predictions may be testable, as was done for the environmental richness test against Alpert's (1999) work on *F. chilensis*. We have also seen how the similarities and the differences between plant foraging theory and the animal foraging literature, and how those similarities and differences can be enlightening. So we are reminded of Lamarck, and his question regarding the fundamental difference between plants and animals. The conclusion of this study is that in the context of foraging, the differences are a matter of scale in the temporal dimension, and a matter of modularity.



APPENDIX A: LITERATURE REVIEW RESULTS

The table that follows (Table 8) contains the entirety of the collected data. For full details of the criteria for acceptance or rejection from the dataset please consult the methods chapter. Source numbers refer to the table at the end of this appendix.

Notation

Foraging response

With respect to the nutrient treatments, N and S indicate non-selective and selective (reduced red:far red ratio) light treatments, respectively. The responses are noted with respect to increasing resource supply; a + indicates either increased internode length or branching frequency in a high light treatment, etc. Zeroes indicate no statistical difference between treatments.

Physiological integration

The integration data indicate a resource and a direction. The direction is noted as A for acropetal, B for basipetal, and F for facultative. A (B) indicates primarily acropetal translocation with evidence for some minor amounts of basipetal movement reported.

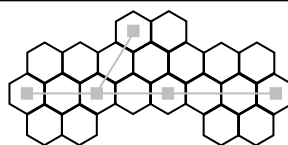
Natural history

The biome classifications begin with T for temperate, Tr for tropical, and A for alpine. Perennials are noted by "Per" and Pseudoannuals by "Pseudo." X and M indicate xeric or mesic water requirements. R and S show clonal method (rhizome or stolon).

Sources

Table A.2 All sources listed in the review table appear here, by number. The full citations appear in the bibliography.

No. Source	No. Source	No. Source
1 Abrahamson et al. (1991)	41 Evans (1992)	81 Noble & Marshall (1983)
2 Adachi <i>et al.</i> (1996a)	42 Evans & Whitney (1992)	82 Noble <i>et al.</i> (1979)
3 Adachi <i>et al.</i> (1996b)	43 Geber <i>et al.</i> (1997)	83 Peñalosa (1983)
4 Aeschmann & Burdet (1994)	44 Ginzo & Lovell (1973a)	84 Piqueras & Klimeš (1998)
5 Alpert (1989)	45 Ginzo & Lovell (1973b)	85 Prati <i>et al.</i> (1997)
6 Alpert (1991)	46 Gleason (1952)	86 Price & Hutchings (1992a)
7 Alpert (1996)	47 Griffith (1998)	87 Price <i>et al.</i> (1992)
8 Alpert & Mooney (1986)	48 Hartnett (1993)	88 Quereshi & Spanner (1971)
9 Angevine & Handel (1986)	49 Hartnett & Bazzaz (1983)	89 Rogan & Smith (1974)
10 Ashmun et al. (1982)	50 Headley <i>et al.</i> (1988a)	90 Room (1983)
11 Bell (1979)	51 Headley <i>et al.</i> (1988b)	91 Rydberg (1965)
12 Brewer & Bertness (1996)	52 Hester <i>et al.</i> (1993)	92 Sackville Hamilton (1980)
13 Brooker <i>et al.</i> (1999)	53 Hickman (1993)	93 Salzman & Parker (1985)
14 Cain (1990)	54 Hoshino (1974)	94 Schmid & Bazzaz (1992)
15 Cain (1994)	55 Huber (1996)	95 Schmid et al. (1988)
16 Cain & Damman (1997)	56 Huber & Hutchings (1997)	96 Shirreffs & Bell (1984)
17 Caradus & Chapman (1991)	57 Huber & Stuefer (1997)	97 Shumway (1995)
18 Caradus <i>et al.</i> (1993)	58 Huber & Wiggerman (1997)	98 Silva (1978)
19 Carlsson & Callaghan (1990)	59 Huber-Sannwald <i>et al.</i> (1998)	99 Slade & Hutchings (1987a)
20 Clapham <i>et al.</i> (1962)	60 Humphrey & Pyke (1997)	100 Slade & Hutchings (1987b)
21 Clifford <i>et al.</i> (1973)	61 Jerling (1988)	101 Slade & Hutchings (1987c)
22 Collins & Oechel (1974)	62 Jónsdóttir & Callaghan (1988)	102 Smith & Palmer (1976)
23 Cook (1988)	63 Jónsdóttir & Callaghan (1989)	103 Sobey & Barkhouse (1977)
24 D'Hertefeldt & Jónsdóttir (1994)	64 Jónsdóttir & Callaghan (1990)	104 Solangaarachchi & Harper (1987)
25 D'Hertefeldt & Jónsdóttir (1999)	65 Jónsdóttir & Watson (1997)	105 Stoll et al. (1998)
26 de Kroon & Knops (1990)	66 Kembal & Marshall (1994)	106 Stuefer & Huber (1998)
27 de Kroon <i>et al.</i> (1991)	67 Kembal & Marshall (1995)	107 Stuefer & Hutchings (1994)
28 de Kroon <i>et al.</i> (1996)	68 Klimeš (1992)	108 Stuefer <i>et al.</i> (1994)
29 de Kroon <i>et al.</i> (1998)	69 Kron & Stewart (1994)	109 Stuefer <i>et al.</i> (1996)
30 Dixon & Jameson (1896)	70 Landa <i>et al.</i> (1992)	110 Svensson <i>et al.</i> (1994)
31 Dong (1993)	71 Lau & Young (1988)	111 Thomas <i>et al.</i> (1990)
32 Dong (1995)	72 Leeflang <i>et al.</i> (1998)	112 Thompson & Harper (1988)
33 Dong & de Kroon (1994)	73 Lotscher & Hay (1997)	113 Tietema (1980)
34 Dong & Pierdominici (1995)	74 Lovett Doust (1981a)	114 Tietema & van der Aa (1981)
35 Dong <i>et al.</i> (1996)	75 Lovett Doust (1981b)	115 Tutin <i>et al.</i> (1993)
36 Dong <i>et al.</i> (1997)	76 Lovett Doust (1987)	116 Tybjerg & Vestergaard (1992)
37 Eckstein & Karlsson (1999)	77 Macdonald & Lieffers (1993)	117 Wijesinghe (1994)
38 Eriksson (1986)	78 Magda <i>et al.</i> (1988)	118 Wijesinghe & Hutchings (1996)
39 Evans (1988)	79 Mitchell & Woodward (1988)	119 Williams (1971)
40 Evans (1991)	80 Newell (1982)	



APPENDIX B: SIMULATION RESULTS

Table B.1 Results from the simulation test of plasticity. CV indicates the coefficient of variation. In any cell with two numbers, the upper is the mean and the lower the standard error for that particular parameter. Values shown are from 200 runs.

ϕ_p	λ_p	B	CV	s	CV	W_g	CV	M	CV	D_g	CV	C_g	CV
0	0	1.430 0.003	2.6	0.333 0.001	6.2	1.551 0.024	22.0	0.301 0.001	5.9	56.09 0.20	5.0	0.065 0.000	7.7
0.1	0	1.422 0.002	2.3	0.338 0.001	6.0	1.480 0.023	21.7	0.297 0.001	5.5	56.41 0.20	5.1	0.063 0.000	8.0
0.25	0	1.390 0.002	2.2	0.347 0.001	6.0	1.365 0.027	27.6	0.281 0.001	5.5	56.19 0.21	5.3	0.061 0.001	9.8
0.5	0	1.311 0.002	2.2	0.362 0.001	5.5	1.179 0.037	44.9	0.237 0.001	6.9	56.61 0.22	5.6	0.056 0.001	18.2
0	1	1.519 0.001	0.8	0.361 0.001	5.6	18.917 0.239	17.9	0.342 0.000	1.6	70.43 0.31	6.2	0.250 0.001	5.9
0.1	1	1.495 0.001	0.9	0.371 0.002	6.4	17.676 0.278	22.2	0.331 0.000	1.7	68.69 0.33	6.8	0.240 0.001	6.7
0.25	1	1.457 0.001	0.9	0.384 0.001	5.1	15.843 0.306	27.3	0.314 0.001	2.0	67.23 0.33	6.9	0.224 0.001	9.0
0.5	1	1.373 0.001	1.1	0.412 0.001	4.9	10.803 0.296	38.7	0.272 0.001	3.0	63.10 0.31	7.0	0.183 0.002	14.2

Table B.2 Results from the plasticity by patch size simulation test. CV indicates the coefficient of variation. In any cell with two numbers, the upper is the mean and the lower the standard error for that particular parameter. Where a standard error is missing, no variation was found. Values shown are from 200 runs.

ϕ_p	λ_p	S	B	CV	s	CV	W_g	CV	M	CV	D_g	CV	C_g	CV
0	0	1	1.452 0.002	2.3	0.329 0.001	2.8	1.43 0.01	14.1	0.312 0.001	5.0	53.59 0.12	3.0	0.064 0.000	5.3
0	0	3	1.433 0.003	2.5	0.333 0.001	6.1	1.50 0.02	18.5	0.302 0.001	5.6	56.02 0.28	4.6	0.064 0.000	6.7
0	1	1	1.521 0.001	0.8	0.329 0.001	1.5	17.01 0.19	15.7	0.343 0.000	1.4	62.66 0.14	3.1	0.248 0.001	5.1
0	1	3	1.519 0.001	0.8	0.363 0.002	6.1	1.92 0.28	20.8	0.342 0.000	1.5	70.12 0.30	6.1	0.251 0.001	7.3
0.25	0	1	1.434 0.002	2.1	0.330 0.001	2.8	1.28 0.02	20.2	0.303 0.001	4.8	53.99 0.12	3.1	0.061 0.000	7.3
0.25	0	3	1.390 0.002	0.2	0.345 0.001	6.0	1.41 0.03	29.4	0.281 0.001	5.7	56.95 0.21	5.3	0.062 0.000	10.2
0.25	1	1	1.467 0.001	0.7	0.330 0.001	1.8	12.49 0.21	23.4	0.319 0.000	1.5	60.19 0.13	3.0	0.217 0.001	8.2
0.25	1	3	1.456 0.001	0.9	0.384 0.001	5.3	15.20 0.30	28.2	0.313 0.000	2.0	67.08 0.31	6.5	0.222 0.001	8.8

Table B.3 Results from the plasticity by patch turnover simulation test. CV indicates the coefficient of variation. In any cell with two numbers, the upper is the mean and the lower the standard error for that particular parameter. Values shown are from 200 runs.

ϕ_p	λ_p	T	B	CV	s	CV	W_g	CV	M	CV	D_g	CV	C_g	CV
0	0	0	1.433 0.002	2.4	0.332 0.001	6.0	1.53 0.02	21.7	0.302 0.001	5.4	56.17 0.20	5.1	0.065 0.000	7.8
0	0	0.10	1.450 0.002	2.1	0.505 0.001	4.0	3.05 0.04	18.2	0.310 0.001	4.7	63.42 0.18	4.1	0.084 0.000	7.2
0	1	0	1.518 0.001	0.8	0.363 0.002	5.9	18.84 0.029	22.1	0.310 0.000	1.6	70.01 0.29	5.9	0.248 0.001	7.6
0	1	0.10	1.636 0.001	1.0	0.504 0.002	4.3	32.23 0.26	11.4	0.389 0.000	1.5	62.92 0.20	4.4	0.288 0.001	4.3
0.25	0	0	1.392 0.003	2.5	0.344 0.001	5.8	1.34 0.03	26.9	0.282 0.001	6.4	56.34 0.21	5.2	0.060 0.000	9.6
0.25	0	0.10	1.443 0.002	2.2	0.504 0.001	3.7	3.32 0.05	21.5	0.307 0.001	4.8	63.89 0.20	4.5	0.087 0.001	8.7
0.25	1	0	1.456 0.001	0.9	0.504 0.001	4.9	15.99 0.30	26.9	0.313 0.000	1.9	67.15 0.29	6.1	0.224 0.001	8.6
0.25	1	0.10	1.634 0.001	1.1	0.507 0.001	3.7	34.56 0.31	12.5	0.388 0.000	1.7	62.40 0.20	4.5	0.295 0.001	4.7
0.50	0	0	1.306 0.002	2.1	0.359 0.001	5.9	1.14 0.03	42.9	0.235 0.001	6.6	56.63 0.23	5.6	0.055 0.001	18.6
0.50	0	0.10	1.416 0.002	1.9	0.501 0.001	3.4	3.30 0.05	22.1	0.294 0.001	4.6	64.27 0.20	4.4	0.087 0.001	8.7
0.50	1	0	1.376 0.001	1.2	0.414 0.001	4.2	10.89 0.34	43.5	0.274 0.001	3.1	63.11 0.34	7.6	0.182 0.002	17.8
0.50	1	0.10	1.626 0.001	1.1	0.505 0.001	4.1	35.33 0.34	13.8	0.385 0.001	1.8	61.72 0.21	4.7	0.297 0.001	5.1

Table B.4 Results from the integration simulation test. CV indicates the coefficient of variation. In any cell with two numbers, the upper is the mean and the lower the standard error for that particular parameter. Values shown are from 20 runs.

Int	ξ_i	B	CV	s	CV	W_g	CV	M	CV	D_g	CV	C_g	CV
Off	0	1.432 0.002	2.4	0.331 0.001	5.9	1.55 0.02	19.7	0.302 0.001	05.5	56.13 0.22	5.6	0.065 0.000	7.2
Avg	1	1.444 0.002	2.1	0.329 0.001	4.0	22.92 4.10	252.7	0.307 0.001	04.7	80.99 0.25	4.4	0.167 0.001	7.3
Avg	2	1.450 0.002	2.1	0.330 0.001	4.9	0.49 0.01	41.7	0.311 0.001	04.6	65.53 0.34	7.3	0.096 0.001	16.7
Avg	3	1.431 0.002	2.3	0.334 0.001	6.1	0.13 0.00	15.5	0.302 0.001	05.2	56.26 0.18	4.6	0.065 0.000	7.2
Avg	4	1.425 0.002	2.4	0.336 0.001	6.0	0.12 0.00	15.6	0.298 0.001	05.7	55.98 0.19	4.8	0.064 0.000	7.1
Avg	5	1.430 0.003	2.6	0.331 0.001	5.7	0.12 0.00	17.2	0.301 0.001	06.0	56.15 0.22	5.6	0.065 0.000	8.0

Table B.5 Results from the integration by patch turnover rate simulation test. CV indicates the coefficient of variation. In any cell with two numbers, the upper is the mean and the lower the standard error for that particular parameter. Values shown are from 200 runs.

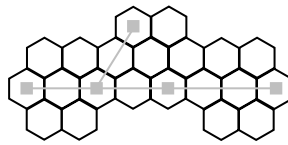
Int	ξ_i	T	B	CV	s	CV	W_g	CV	M	CV	D_g	CV	C_g	CV
0	0	0	1.429 0.003	2.6	0.333 0.001	5.8	1.51 0.02	17.0	0.300 0.001	6.0	56.11 0.20	5.1	0.064 0.000	6.6
0	0	0.5	1.431 0.002	2.3	0.334 0.001	6.1	0.13 0.00	15.5	0.302 0.001	5.2	56.26 0.18	4.6	0.065 0.000	7.2
0	0	0.10	1.425 0.002	2.4	0.336 0.001	6.0	0.12 0.00	15.6	0.298 0.001	5.7	55.98 0.19	4.8	0.064 0.000	7.1
Avg	2	0	1.450 0.002	2.0	0.331 0.001	5.2	0.51 0.02	45.9	0.311 0.001	4.4	66.04 0.32	6.8	0.097 0.001	16.1
Avg	2	0.5	1.460 0.002	1.9	0.498 0.001	3.2	5.88 2.07	498.6	0.315 0.001	4.1	78.46 0.23	4.2	0.151 0.001	8.3
Avg	2	0.10	1.475 0.002	1.9	0.500 0.001	2.8	4.74 1.02	304.6	0.314 0.001	4.0	78.95 0.22	3.9	0.154 0.001	9.7
Avg	5	0	1.432 0.002	2.3	0.334 0.002	6.4	0.12 0.00	15.8	0.302 0.004	5.3	56.28 0.20	5.1	0.064 0.000	7.2
Avg	5	0.5	1.451 0.002	1.9	0.504 0.001	4.1	0.21 0.00	14.1	0.311 0.001	4.3	63.95 0.21	4.7	0.082 0.000	6.8
Avg	5	0.10	1.452 0.002	1.8	0.502 0.001	3.5	0.22 0.00	12.9	0.312 0.001	4.0	63.77 0.20	4.5	0.084 0.000	6.5

Table B.6 Results from the integration by environmental richness simulation test. CV indicates the coefficient of variation. In any cell with two numbers, the upper is the mean and the lower the standard error for that particular parameter. Values shown are from 200 runs.

Int	ξ_i	F_A, F_B	B	CV	s	CV	W_g	CV	M	CV	D_g	CV	C_g	CV
Off	0	0.25	1.443 0.002	2.3	0.474 0.002	4.8	1.94 0.02	16.4	0.307 0.001	5.2	59.42 0.21	5.0	0.064 0.000	6.3
Off	0	0.50	1.450 0.002	1.8	0.504 0.001	3.9	2.91 0.05	23.0	0.310 0.001	4.0	64.49 0.26	5.6	0.065 0.000	8.6
Off	0	0.75	1.458 0.002	1.8	0.536 0.001	3.4	4.90 0.09	26.9	0.314 0.001	3.9	71.74 0.28	5.6	0.064 0.000	10.8
Avg	2	0.25	1.463 0.002	1.9	0.466 0.001	3.6	1.31 0.03	29.9	0.316 0.001	4.0	71.87 0.25	5.0	0.097 0.001	9.7
Avg	2	0.50	1.461 0.002	1.7	0.500 0.001	2.8	13.76 3.57	367.4	0.316 0.001	3.7	79.49 0.28	4.9	0.151 0.001	10.3
Avg	2	0.75	1.459 0.002	1.7	0.532 0.001	2.7	163.40 18.87	163.4	0.315 0.001	3.7	87.16 0.30	4.9	0.154 0.001	7.3
Avg	5	0.25	1.447 0.002	2.2	0.472 0.001	4.5	0.15 0.00	14.3	0.309 0.001	4.9	59.40 0.21	5.1	0.064 0.000	6.8
Avg	5	0.50	1.452 0.002	2.0	0.505 0.001	3.9	0.20 0.00	17.8	0.311 0.001	4.4	64.71 0.26	5.6	0.082 0.000	8.6
Avg	5	0.75	1.460 0.002	1.6	0.536 0.001	2.9	0.32 0.00	21.6	0.315 0.001	3.5	71.66 0.28	5.6	0.084 0.000	10.8

ϕ_p	λ_p	ξ_i	Cov	T	P	B	CV	s	CV	W_g	CV	M	CV	D_g	CV	C_g	CV
0.25	1	0	-	0.01	3	1.475 0.001	0.9	0.249 0.001	5.6	8.75 0.18	29.8	0.322 0.000	1.9	62.16 0.05	1.0	0.205 0.002	11.6
0.25	1	0	-	0.10	3	1.588 0.001	0.8	0.255 0.001	5.7	18.56 0.25	19.0	0.370 0.000	1.3	62.29 0.03	0.7	0.274 0.001	7.0
0.25	1	0	+	0.01	3	1.502 0.001	1.0	0.547 0.002	4.7	46.29 0.43	13.2	0.334 0.001	1.9	69.48 0.29	5.9	0.336 0.001	4.9
0.25	1	0	+	0.10	3	1.587 0.001	0.9	0.511 0.002	4.8	63.23 0.45	10.2	0.370 0.000	1.5	68.27 0.21	4.3	0.388 0.001	4.2
0.25	1	0	0	0.01	1	1.595 0.001	0.7	0.447	1.2	16.84 0.27	23.1	0.373 0.000	1.1	56.55 0.13	3.3	0.252 0.001	8.4
0.25	1	0	0	0.10	1	1.675 0.001	0.9	0.500	1.0	31.45 0.02	12.3	0.403 0.000	1.3	57.17 0.13	3.3	0.296 0.001	4.5
0.25	1	2	-	0.01	3	1.475 0.001	0.9	0.248 0.001	6.1	1.21 0.03	33.6	0.322 0.000	1.9	62.09 0.05	1.2	0.202 0.002	14.7
0.25	1	2	-	0.10	3	1.583 0.001	0.8	0.252 0.001	5.7	2.72 0.03	17.6	0.369 0.000	1.3	62.18 0.03	0.8	0.269 0.001	6.0
0.25	1	2	+	0.01	3	1.550 0.001	0.7	0.539 0.001	3.6	644.60 117.90	258.5	0.355 0.000	1.2	81.63 0.30	5.2	0.606 0.004	9.7
0.25	1	2	+	0.10	3	1.635 0.001	0.6	0.507 0.001	3.7	531.60 65.72	174.8	0.389 0.000	1.0	85.61 0.25	4.1	0.719 0.003	5.9
0.25	1	2	0	0.01	1	1.582 0.001	0.7	0.447	1.1	3.83 0.08	28.9	0.368 0.000	1.2	60.63 0.18	4.1	0.300 0.003	12.5
0.25	1	2	0	0.10	1	1.695 0.001	0.6	0.500	0.7	22.95 0.37	22.8	0.410 0.000	0.8	72.73 0.19	3.7	0.530 0.003	8.7
0	0	0	-	0.01	3	1.412 0.003	3.4	0.230 0.001	7.4	0.99 0.01	10.8	0.291 0.002	8.5	50.00 0.00	0	0.055 0.000	3.8
0	0	0	-	0.10	3	1.405 0.003	3.2	0.249 0.001	6.7	1.01 0.01	11.2	0.288 0.002	8.0	50.00 0.00	0	0.055 0.000	3.9
0	0	0	+	0.01	3	0.146 0.002	1.7	0.483 0.002	4.9	4.92 0.08	22.3	0.315 0.010	3.8	74.57 0.27	5.1	0.109 0.001	8.8
0	0	0	+	0.10	3	1.461 0.002	1.6	0.505 0.002	4.5	8.40 1.51	254.9	0.316 0.001	3.5	76.88 0.24	4.4	0.125 0.001	7.3
0	0	0	0	0.01	1	1.458 0.002	2.3	0.448 0.001	2.0	1.53 0.01	11.6	0.314 0.001	5.0	54.16 0.11	2.8	0.065 0.000	4.4
0	0	0	0	0.10	1	1.478 0.002	1.9	0.500 0.001	1.6	2.62 0.02	12.0	0.324 0.001	3.9	59.88 0.14	3.3	0.080 0.000	4.8
0	0	2	-	0.01	3	1.410 0.003	3.1	0.231 0.001	7.8	0.20 0.00	13.8	0.291 0.002	7.4	51.05 0.11	3.1	0.056 0.000	4.4
0	0	2	-	0.10	3	1.407 0.003	3.4	0.248 0.001	7.0	0.24 0.00	12.6	0.289 0.002	8.2	50.00 0.00	0	0.055 0.000	3.9
0	0	2	+	0.01	3	1.464 0.002	1.6	0.475 0.001	4.3	29.76 6.88	327.2	0.317 0.001	3.4	82.15 0.30	5.1	0.162 0.001	9.5
0	0	2	+	0.10	3	1.459 0.002	1.8	0.499 0.001	3.8	85.88 11.01	181.2	0.315 0.001	3.9	85.83 0.24	3.9	0.179 0.001	5.7
0	0	2	0	0.01	1	1.473 0.002	1.9	0.447 0.001	1.7	0.83 0.01	21.3	0.321 0.001	4.0	66.52 0.16	3.3	0.110 0.001	7.7
0	0	2	0	0.10	1	1.469 0.002	1.6	0.500	1.3	2.29 0.03	21.1	0.319 0.001	3.4	76.21 0.18	3.3	0.150 0.001	8.0

Table B.7 (previous page) Results from the simulation test of foraging and integration against environmental predictability. CV indicates the coefficient of variation. In any cell with two numbers, the upper is the mean and the lower the standard error for that particular parameter. An absent standard error indicates that no variation was found in the simulation's output for those runs. Values shown are from 200 runs.



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