Consequences of Architecture and

Resource Allocation for

Growth Dynamics of Bunchgrass Clones

by

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Abstract

In order to understand how bunchgrasses achieve dominance over other plant growth forms and how they achieve dominance over one another in different environments, it is first necessary to develop a detailed understanding of how their growth strategy interacts with the resource limits of their environment. Two properties which have been studied separately in limited detail are architecture and disproportionate resource allocation. Architecture is the structural layout of organs and objects at different hierarchical levels. Disproportionate resource allocation is the manner in which resources are allocated across objects at each level of hierarchy. Clonal architecture and disproportionate resource allocation may interact significantly to determine the growth ability of clonal plants. These interactions have not been researched in bunchgrasses.

This thesis employs a novel simulation technique, functional-structural plant modelling, to investigate how bunchgrasses interact with the resource constraints imposed in humid grasslands. An appropriate functional-structural plant model, the TILLERTREE model, is developed that integrates the architectural growth of bunchgrasses with environmental resource capture and disproportionate resource allocation. Simulations are conducted using a chosen model species *Themeda triandra*, and the environment is parameterised using characteristics of the Southern Tall Grassveld, a humid grassland type found in South Africa. Behaviour is considered at two levels, namely growth of single ramets and growth of multiple ramets on single bunchgrass clones.

In environments with distinct growing and non-growing seasons, bunchgrasses are subjected to severe light depletion during regrowth at the start of each growing season because of the accumulation of dead material in canopy caused by the upright, densely-packed manner in which they grow. Simulations conducted here indicate that bunchgrass tillers overcome this resource bottleneck through structural adaptations (etiolation, non-linear blade mass accretion, residual live photosynthetic surface) and disproportionate resource allocation between roots and shoots of individual ramets that together increase the temporal resource efficiency of ramets by directing more resources to shoot growth and promoting extension of new leaves through the overlying dead canopy.

The architectural arrangement of bunchgrasses as collections of tillers and ramets directly leads to consideration of a critical property of clonal bunchgrasses: tiller

recruitment. Tiller recruitment is a fundamental discrete process limiting the vegetative growth of bunchgrass clones. Tiller recruitment occurs when lateral buds on parent tillers are activated to grow. The mechanism that controls bud outgrowth has not been elucidated. Based on a literature review, it is here proposed that lateral bud outgrowth requires suitable signals for both carbohydrate and nitrogen sufficiency. Subsequent simulations with the model provide corroborative evidence, in that greatest clonal productivity is achieved when both signals are present.

Resource allocation between live structures on clones may be distributed proportionately in response to sink demand or disproportionately in response to relative photosynthetic productivity. Model simulations indicate that there is a trade-off between total clonal growth and individual tiller growth as the level of disproportionate allocation between ramets on ramet groups and between tillers on ramets increases, because disproportionate allocation reduces tiller population size and clonal biomass, but increases individual tiller performance. Consequently it is proposed that different life strategies employed by bunchgrasses, especially annual versus perennial life strategies, may follow more proportionate and less proportionate allocation strategies respectively, because the former favours maximal resource capture and seed production while the latter favours individual competitive ability.

Structural disintegration of clones into smaller physiologically integrated units (here termed ramet groups) that compete with one another for resources is a documented property of bunchgrasses. Model simulations in which complete clonal integration is enforced are unable to survive for long periods because resource bottlenecks compromise all structures equally, preventing them from effectively overcoming resource deficits during periods when light is restrictive to growth. Productivity during the period of survival is also reduced on bunchgrass clones with full integration relative to clones that disintegrate because of the inefficient allocation of resources that arises from clonal integration. This evidence indicates that clonal disintegration allows bunchgrass clones both to increase growth efficiency and pre-empt potential death, by promoting the survival of larger ramet groups and removing smaller ramet groups from the system.

The discrete nature of growth in bunchgrasses and the complex population dynamics that arise from the architectural growth and the temporal resource dynamics of the environment, may explain why different bunchgrass species dominate under different environments. In the final section this idea is explored by manipulating two species tiller traits that have been shown to be associated with species distributions across non-selective

defoliation regimes, namely leaf organ growth rate and tiller size (mass or height). Simulations with these properties indicate that organ growth rate affects daily nutrient demands and therefore the rate at which tillers are terminated, but had only a small effect on seasonal resource capture. Tiller mass size affects the size of the live tiller population where smaller tiller clones maintain greater numbers of live tillers, which allows them to them to sustain greater biomass over winter and therefore to store more reserves for spring regrowth, suggesting that size may affect seasonal nitrogen capture. The greatest differences in clonal behaviour are caused by tiller height, where clones with shorter tillers accumulate substantially more resources than clones with taller tillers. This provides strong evidence there is trade-off for bunchgrasses between the ability to compete for light and the ability to compete for nitrogen, which arises from their growth architecture.

Using this evidence it is proposed that bunchgrass species will be distributed across environments in response to the nitrogen productivity. Shorter species will dominate at low nitrogen productivity, while taller species dominate at high nitrogen productivity. Empirical evidence is provided in support of this proposal.

Preface

The work described in this dissertation was carried out in the School of Mathematical Sciences (formerly the School of Mathematics, Statistics and Information Technology) at the University of KwaZulu-Natal, Pietermaritzburg, from March 1999 to January 2005, under the supervision of Professor TG O'Connor (School of Applied Environmental Sciences, University of KwaZulu-Natal 1999 - 2001; School of Animal, Plant and Environmental Sciences, University of the Witwatersrand 2001 – 2005), Professor JW Hearne (School of Mathematics, Statistics and Information Technology, University of KwaZulu-Natal 1999 - 2002; School of Mathematical and Geospatial Sciences, Royal Melbourne Institute of Technology, 2003 - 2005), and Professor Johan Swart (School of Mathematics, Statistics and Information Technology, University of KwaZulu-Natal 2003 – 2004; School of Mathematical Sciences, University of KwaZulu-Natal 2005).

These studies present original work by the author and have not otherwise been submitted in any form to another university. Where use has been made of the work of others it has been duly acknowledged.

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Date 22/7/2005

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Professor T.G. O'Connor (Supervisor)

Table of Contents

List of Abbreviations and Symbols

This section includes abbreviations and descriptive names for variables used in the model. Where a contextual description is considered necessary, a section reference is provided.

1   MISCELLANEOUS

t	iteration (discrete time, Δt)
	(TILLERTREE model uses a day iteration, so all equations are solved as difference equations.)
Yearday	day in a solar year calculated from the 1 September (= Yearday 1)
Gregday	day in a solar year calculated from 1 January (= Gregday 1)

2   ARCHITECTURAL VARIABLES AND PARAMETERS   (CHAPTER 2)

2.1   Objects

α	phytomer
β	tiller
γ	ramet
δ	ramet group

2.2   Organs

o	organ (generic term including: blade, sheath, internode, flower, root)
b	blade
s	sheath
in	internode
f	flower
r	root
i	species (identifies species parameters)

h	height class

2.3 Organ variables and parameters

$llo_{\alpha,t}$	organ actual live length (state variable) (mm) (Ch 2, Section 3)
$ldo_{\alpha,t}$	organ actual dead length (state variable) (mm) (Ch 2, Section 3)
$wlo_{\alpha,t}$	organ live mass (state variable) (g DM) (Ch 2, Section 3)
$wdo_{\alpha,t}$	organ dead mass (state variable) (g DM) (Ch 2, Section 3)
$max\Psi llo_i$	organ maximum potential length (mm) (Ch 2, Section 3)
$max\Psi gllo_i$	organ maximum potential daily length growth rate (mm d^{-1}) (Ch 2, Section 3)
$\Psi gllo_{\alpha,t}$	organ potential daily length growth rate (environmental limitation) (mm d^{-1}) (Ch 2, Section 3)
$gllo_{\alpha,t}$	organ actual daily length growth (resource limitation) (mm) (Ch 2, Section 3)
$\Psi llo_{\alpha,t}$	organ potential length thus far (environmental limitation) (mm) (Ch 2, Section 3)
$maxllo_{\alpha,t}$	organ maximum achieved length so far (mm) (Ch 2, Section 3)
$max\Psi dllo_i$	organ maximum potential daily length dieback rate (mm d^{-1}) (Ch 2, Section 3)
$dllo_{\alpha,t}$	organ actual daily length dieback (resource limitation) (mm) (Ch 2, Section 3)
$deldo_{\alpha,t}$	organ actual daily length decay (mm) (Ch 2, Section 3)
$Rdecay_i$	decay rate of dead matter (g g^{-1} or mm mm^{-1}) (Ch 2, Section 3)
$cllo_{\alpha,t}$	organ live material removed by defoliation event (mm) (Ch 2, Section 3)
$cldo_{\alpha,t}$	organ dead material removed by defoliation event (mm) (Ch 2, Section 3)
$\Psi gwlo_{\alpha,t}$	organ actual daily mass growth rate (g DM d^{-1}) (Ch 2, Section 4)
$max\Psi gwlo_i$	organ maximum potential daily mass growth rate (g g^{-1} d^{-1}) (Ch 2, Section 4)
$awllo_i$	organ live mass to length ratio (g mm^{-1}) (Ch 2, Section 3)
$maxawllo_i$	maximum organ live mass to length ratio (g DM mm^{-1}) (Ch 7, Section 1)
$minawllo_i$	minimum organ live mass to length ratio (g DM mm^{-1})

x

	(Ch 7, Section 1)
$awAo_i$	specific organ area or mass-to-area ratio (g DM cm^{-2}) (Ch 3)
ρo_i	organ density (g DM mm^{-3}) (Ch 3)
$awlo_i$	organ daily mass increment (g g^{-1} d^{-1}) (Ch 2, Section 3)
$dwlo_{\alpha,t}$	organ daily mass dieback (g g^{-1} d^{-1}) (Ch 2, Section 3)
$adlo_i$	organ fractional death rate (g g^{-1} d^{-1}) (Ch 2, Section 3)
$awdo_i$	organ proportional dead mass loss (g g^{-1}) (Ch 2, Section 3)
$\Omega alrlsh_{\gamma,t}$	ideal live root to shoot ratio (dimensionless) (Ch 2, Section 4)
$alrlsh_{\gamma,t}$	actual live root to shoot ratio (dimensionless) (Ch 2, Section 4)
$maxalrlsh_i$	maximum live root to shoot ratio (dimensionless) (Ch 2, Section 4)
$minalrlsh_i$	minimum live root to shoot ratio (dimensionless) (Ch 2, Section 4)

3   CURRENCY VARIABLES AND PARAMETERS   (CHAPTER 3)

3.1   Ramet variables and parameters

C	carbon
CHO	carbohydrate
N	nitrogen
$AVC_{\gamma,\delta,t}$	available unbound non-structural carbohydrate in a ramet (state variable) (g CHO) (Ch 3, Section 1)
$AVN_{\gamma,\delta,t}$	available unbound non-structural nitrogen in a ramet (state variable) (g N) (Ch 3, Section 2)

3.1.1   *Photosynthesis*   (Ch 3, Section 1)

$Pmax_i$	maximum photosynthetic rate per unit leaf blade area (mg CO$_2$ dm^{-2} h^{-1} or g glucose cm^{-2} h^{-1})
$CNetPs_{\gamma,t}$	net photosynthetic production on a ramet (g glucose d^{-1})
$Alb_{\alpha,\beta,\gamma,\delta,t,h}$	organ surface area in height class h (cm^2)
BAl_h	blade area index above height layer h (m m^{-1})

SAI_h	sheath area index above height layer h (m m^{-1})
IAI_h	internode area index above height layer h (m m^{-1})
CAI_h	canopy area index above height layer h (m m^{-1})
$oangle_i$	angle of organ length relative to a horizontal surface (°)
$F_p(oangle_i)$	integral of light absorption as a function of organ angle
K_i	light extinction coefficient
$F_p(CAI_h)$	functional reduction of photosynthesis by light reduction due to overlying canopy area index
$F_p(N)$	functional relationship between photosynthesis and organ N concentration

3.1.2   Nitrogen uptake   (Ch 3, Section 2)

$RNuptake_i$	rate of N uptake from the soil (g N (g wlr)$^{-1}$)
$Nuptake_{\gamma,\delta,t}$	daily N uptake (g N)

3.1.3   Maintenance   (Ch 3, Section 1)

$Cmfrlo_i$	organ carbohydrate requirement for maintenance (g CHO (g DM)$^{-1}$)
$Cmaint_{\gamma,\delta,t}$	total maintenance demand of the ramet at time t (g CHO)

3.1.4   Growth   (Ch 3, Section 1.2 & Section 2)

$Cgrow_{\gamma,\delta,t}$	total growth demand of the ramet at time t (g CHO)
$aCgo_i$	organ growth conversion rate (g CHO (g DM)$^{-1}$)
$Ngrow_{\gamma,\delta,t}$	total growth demand of the ramet at time t (g N)
$aNgo_i$	organ growth conversion rate (g N (g DM)$^{-1}$)

3.1.5   Storage   (Ch 3, Section 1 & Section 2)

$Cstore_{o,\alpha,\beta,\gamma,\delta,t}$	actual reserve CHO storage in organ tissue (g CHO (g DM)$^{-1}$)
$\Omega Cstore_{o,\alpha,\beta,\gamma,\delta,t}$	ideal reserve CHO storage in organ tissue (g CHO (g DM)$^{-1}$)
$maxCstore_{i,o}$	maximum possible CHO storage in organ tissue (g CHO (g DM)$^{-1}$)
$minCstore_{i,o}$	minimum possible CHO storage in organ tissue (g CHO (g DM)$^{-1}$)
$RCstore_i$	rate at which CHO may be extracted out of / deposited into Cstorage (g g^{-1})
$\Omega Nstore_{i,o}$	ideal reserve N storage in organ tissue (g N (g DM)$^{-1}$)

$RNstore_i$	rate at which N may be extracted out of Nstorage (g g^{-1})

3.1.6 Senescence (Ch 3, Section 1 & Section 2)

$RCdieback_{i,o}$	CHO recovered per unit dieback of an organ (g CHO (g DM)$^{-1}$)
$Cdieback_{\gamma,\delta,t}$	total CHO recovered from organ senescence by a ramet at time t (g CHO)
$RNdieback_{i,o}$	N recovered per unit dieback of an organ (g N (g DM)$^{-1}$)
$Ndieback_{\gamma,\delta,t}$	total N recovered from organ senescence by a ramet at time t (g N)

3.1.7 Defoliation (Ch 3, Section 1 & Section 2)

$cAVC_{\gamma,\delta,t}$	amount of AVC removed by a defoliation event (g CHO)
$cAVN_{\gamma,\delta,t}$	amount of AVN removed by a defoliation event (g CHO)

3.1.8 Secondary metabolism (Ch 3, Section 1)

$CSecMetab_{\gamma,\delta,t}$	daily amount of CHO converted to secondary metabolite, which is lost to the ramet (g CHO)

3.2 Ramet group variables (Ch 3, Section 3)

$CSupDem_{\delta,t}$	CHO allocated in ramet group to supply demands of connected ramets (g CHO)
$CDem_{\gamma,\delta,t}$	demand for CHO placed by individual ramets (g CHO)
$CExcess_{\delta,t}$	amount of CHO in that exceeds total demands ramets (g CHO)
$NSupDem_{\delta,t}$	N allocated in ramet group to supply demands of connected ramets
$NDem_{\gamma,\delta,t}$	demand for N placed by individual ramets
$NExcess_{\delta,t}$	amount of N in ramet group that exceeds total demands ramets

4 ENVIRONMENTAL VARIABLES

4.1 Temperature (Ch 4, Section 4)

T_{ave} average daily air temperature

T_{min} minimum daily air temperature

$f(T_{ave})$ multiplier function that limits growth, senescence, photosynthesis, and maintenance in response to average air temperature (dimensionless) (Chapter 4)

4.2 Soil water pressure (Ch 4, Section 4)

Ψ_s soil water potential (MPa)

$f_g(\Psi_s)$ multiplier function that limits growth in response to soil water pressure (dimensionless) (Chapter 4)

$f_p(\Psi_s)$ multiplier function that limits photosynthesis in response to soil water pressure (dimensionless) (Chapter 4)

$f_m(\Psi_s)$ multiplier function that limits maintenance in response to soil water pressure (dimensionless) (Chapter 4)

5 DEFOLIATION VARIABLES

gh graze height – height above ground at which a graze defoliation event is applied (mm)

bh burn height – height above ground at which a fire defoliation event is applied (mm)

Chapter 1:   Introduction

Long-term species dominance or even survival in any vegetation type is set by the ecological adaptation of each species with respect to all other species, in the face of ever-varying combinations of the physical and biological environments. Ecological fitness is determined by the individual species traits that are critical to providing plants with a competitive edge in any particular environment (Tilman 1988; Grime 2001). These traits include those important for surviving the physical environment, others for coping with direct competition for limiting resources from neighbouring plants (Lauenroth & Aguilera 1998), and those which enable a plant to survive defoliation.

Grasslands are multi-species communities, consisting of both clonal and non-clonal plants (Hartnett & Fay 1998; O'Connor & Everson 1998; Craine *et al.* 2002). Species distribution in these swards is dependent firstly on the physical environment (climate and soil type), which determines the potential species complement of a site (Tilman 1988), and secondly on the biological environment, particularly neighbour competition for resources and the defoliation regime determined by fire and grazing animals (Woodward 1987; Grime 2001).

We seek a detailed approach for understanding multi-species grassland dynamics. Such an approach needs to consider the individual traits of different grassland species and how they respond to the environments they inhabit, as it is the individual suite of characteristics possessed by each species that determines how it will perform relative to other species in any particular environment. The question then is: what properties of plants are important in defining differences among individual species? These are numerous, but I divide them into two broad categories, namely architectural properties and physiological properties. Plant architecture is defined as the three-dimensional structural organisation of the plant body. For the plant shoot this includes the branching pattern, as well as the size, shape and position of individual organs (Reinhardt & Kuhlemeier 2002). The three-dimensional arrangement of roots can similarly be described in terms of branching elements. For clonal plants, which have the potential to grow separate functioning plants through vegetative propagation, this definition needs to be extended to include relationships among multiple individual plants which each have their own root and shoot systems, that

1

are able to share resources with one another. (Harper 1981) Architecture therefore describes both relative arrangements of plant structures (Barthélémy 1991) that distinguish plant growth forms and individual organ morphological differences between species within growth forms (Reinhardt & Kuhlemeier 2002). Architectural variation among plants is often determined by a small number of attributes including branch angles, internode length, and the probability of bud growth (Harper 1981). Physiological properties are more complex, and relate to internal chemical processes. Obvious examples are differences in photosynthetic pathways (C_3, C_4, CAM) and adaptations to tolerate particular environmental toxins such as high salt concentrations. It also covers allocation of resources to different functions and structures in the plant in response to growth functions (e.g. vegetative versus sexual reproductive growth) and relative resource limitations (e.g. root to shoot allocation) (Thornley & Johnson 1990). Plants are able to allocate resource disproportionately to different structures, which improves their ability to obtain limiting environmental resources within the constraints of their architecture. Therefore interactions between architecture and resource allocation may cause substantial changes to the growth ability of plants and their ability to survive spatial and termporal resource heterogeneity in the environments they occupy. In this thesis, I explore the effects of interactions between architectural characteristics and resource allocation on the behaviour of bunchgrasses.

So what are bunchgrasses? Grasses can be divided into two broad groups based on the manner in which their tillers grow (Briske & Derner 1998). Tillers are individual axes of growth in plant shoots with a leading meristem where leaves and other shoot organs are recruited (Room et al. 1994). Bunchgrasses (tussock grasses) are composed of tillers that grow vertically. Clones of bunchgrasses spread slowly in horizontal space and grow rapidly in vertical space. They are strong competitors for light. This tuft-forming growth strategy is also known as the caespitose growth form. Some grass species in this category are also termed 'stoutly rhizomatous' because they have the ability to form short rhizomes (e.g. Gibbs-Russell et al. 1990). Stoloniferous grasses consist of tillers that grow horizontally along the ground surface. Stoloniferous grasses spread rapidly in open horizontal space and will only grow vertically if forced to do so by the density of surrounding vegetation. They are poor competitors for light, but good at exploiting horizontal spatial heterogeneity of soil nutrients in non-light-limiting environments (Hutchings & de Kroon 1994; Briske & Derner 1998).

Bunchgrasses occur in many vegetation types around the world ranging from arid (Mares 1999) through to humid environments (O'Connor & Bredenkamp 1997; Hartnett &

Fay 1998), from tropical (Coughenour 1984) to temperate zones (Pitt & Hooper 1994), from sea-level to alpine altitudes (O'Connor & Bredenkamp 1997; Uys, Bond & Everson 2004). They appear to be most dominant in sub-humid to humid grasslands (O'Connor & Bredenkamp 1997; Hartnett & Fay 1998; Fynn, Morris & Edwards 2005a). Dominance amongst bunchgrass species changes dramatically in response to non-selective defoliation treatments (Everson & Tainton 1984; Fynn et al. 2005a) and across soil nutrient gradients (Tilman 1988) indicating that individual species' traits have a strong effect on the outcome of competition under different environmental regimes.

This thesis will focus on the growth of bunchgrasses in humid bunchgrass communities. Bunchgrasses are both subject to the climate and soil constraints of the environment they inhabit and also help determine the constraints of the environment they inhabit by the manner in which they grow (Briske & Derner 1998). In the next section, the architecture of bunchgrasses is discussed in detail. Then, a description of limiting resources in humid grasslands is provided. This is followed by a discussion of the architectural and resource allocation adaptations used by bunchgrasses to respond to spatiotemporal variability in resources in humid grasslands.

1 THE ARCHITECTURE OF CLONAL BUNCHGRASSES

Grasses are clonal plants that recruit new plants both sexually and asexually through vegetative reproduction. Shoot structures in grasses are elegantly simple, consisting of collections of tillers. Each tiller is an individual axis of shoot growth composed of substructures called phytomers (Etter 1951; Kurihara et al. 1978; Bell 1991), also known as the metamers (Room, Maillette & Hannan 1994). A phytomer consists of the following discrete organs: leaf blade and sheath, an internode, and an axillary bud at the distal end of the internode (Figure 1.1). Each tiller has a meristem at its leading end where new phytomers are recruited. Therefore the term tiller, which is used in reference to graminoids, is analogous to individual growth axes in all higher plants (Room et al. 1994). Tiller growth is terminated by the formation of flowers.

A tiller is further able to recruit new tillers (termed secondary or daughter tillers) from the axillary buds on each phytomer, which is the method of vegetative reproduction. The rate at which bunchgrasses can increase their biomass is determined by the rate at which existing discrete organs can expand and the rate at which new tillers can be recruited,

3
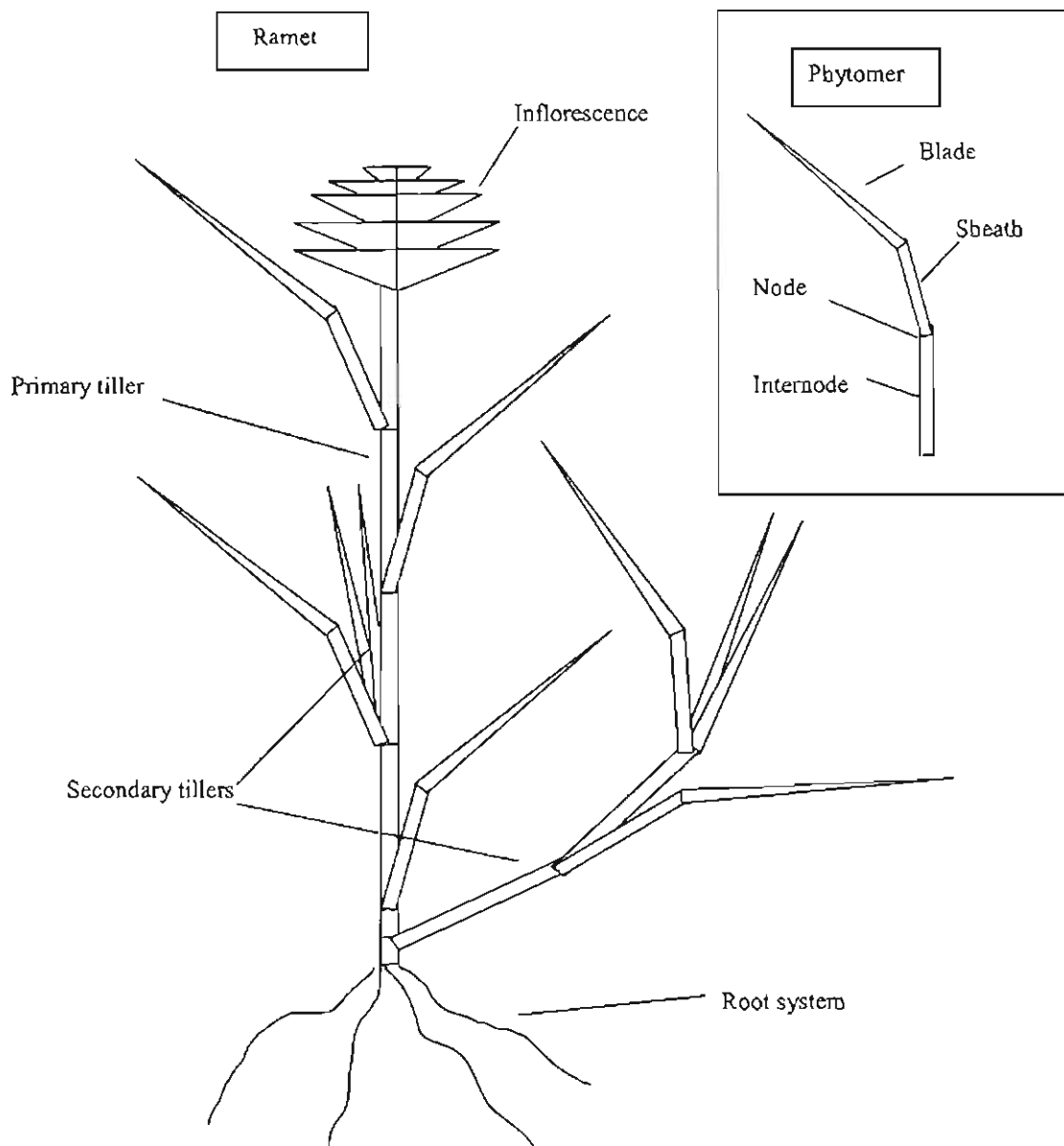
Figure 1.1   Diagram of the structure of a ramet, which represents a functional grass plant. Note that the diagram shows three connected tillers, one parent rooted tiller and two daughter tillers, each of which are composed of a sequence of phytomers. (Inset: diagram of an individual phytomer with its component organs. Each phytomer is composed of a single internode, sheath, blade, and a meristem located at the node. Flowers are usually only associated with terminal phytomers.)

also a discrete process. Therefore it is apparent that growth potential in bunchgrasses is subject to limitations imposed by discrete growth processes in plants: more growing organs means increased total plant potential growth rate and total plant potential growth rate increases stepwise with each growing organ or tiller recruited onto the plant. At any given time, the growth potential of the plant in response to environmental resources is constrained by the abundance of active meristems (Maschinski & Whitham 1989).

Each tiller has the ability to grow its own root system, and is thereby able to become a functioning plant capable of both photosynthesis and soil nutrient capture. Therefore any secondary tiller that does grow its own root system has the potential to survive independently of its parent tiller. These rooted plants capable of independent growth are termed ramets (Harper 1977). It is this ability to form ramets that ensures the potentially indefinite persistence of clonal plants. Bunchgrass ramets may consist of several tillers connected to a single root system via the oldest parent tiller in the group (Gibbs-Russell et al. 1990).

A grass clone, or genet, may be defined as the set of all plant structures descended from a common ancestral zygote (Kays & Harper 1974). Each bunchgrass clonal tuft is not a physiologically integrated unit. Rather physiological integration on a grass tuft is confined to autonomous groups of physiologically connected ramets on the tuft, termed ramet hierarchies (Welker et al. 1987). This partial integration can be explained on the basis of the architectural development of bunchgrass clones descended from a common parent seedling (Figure 1.2). Individual ramets have limited longevity and they may die after flowering, or they may senesce prematurely due to unfavourable environmental conditions. Consequently the daughter ramets of a dead parent ramet are disconnected by this event and hence become competing plants (Briske & Derner 1998). These then form the base plant 'individuals' that are subjected to competition with surrounding autonomous hierarchies within the grass clone as well as to competition with surrounding grass clones. Therefore in bunchgrass communities, there is both inter-clonal resource competition and intra-clonal resource competition. The relative intensities of intra-clonal and inter-clonal competition have been demonstrated to be comparable in several caespitose grasses (Briske & Butler 1989). Hence any attempt to understand growth of individual bunchgrass clones should incorporate this disintegration characteristic of bunchgrasses. For the purposes of this thesis and in order to avoid confusion in the description that follows, I refer to these autonomous hierarchies as ramet groups because 'hierarchy' is a general term used to define structural organisation.

A. Physiological integration on clonal genet prior to death of the parent ramet

B. Formation of autonomous ramet groups after death of the parent ramet
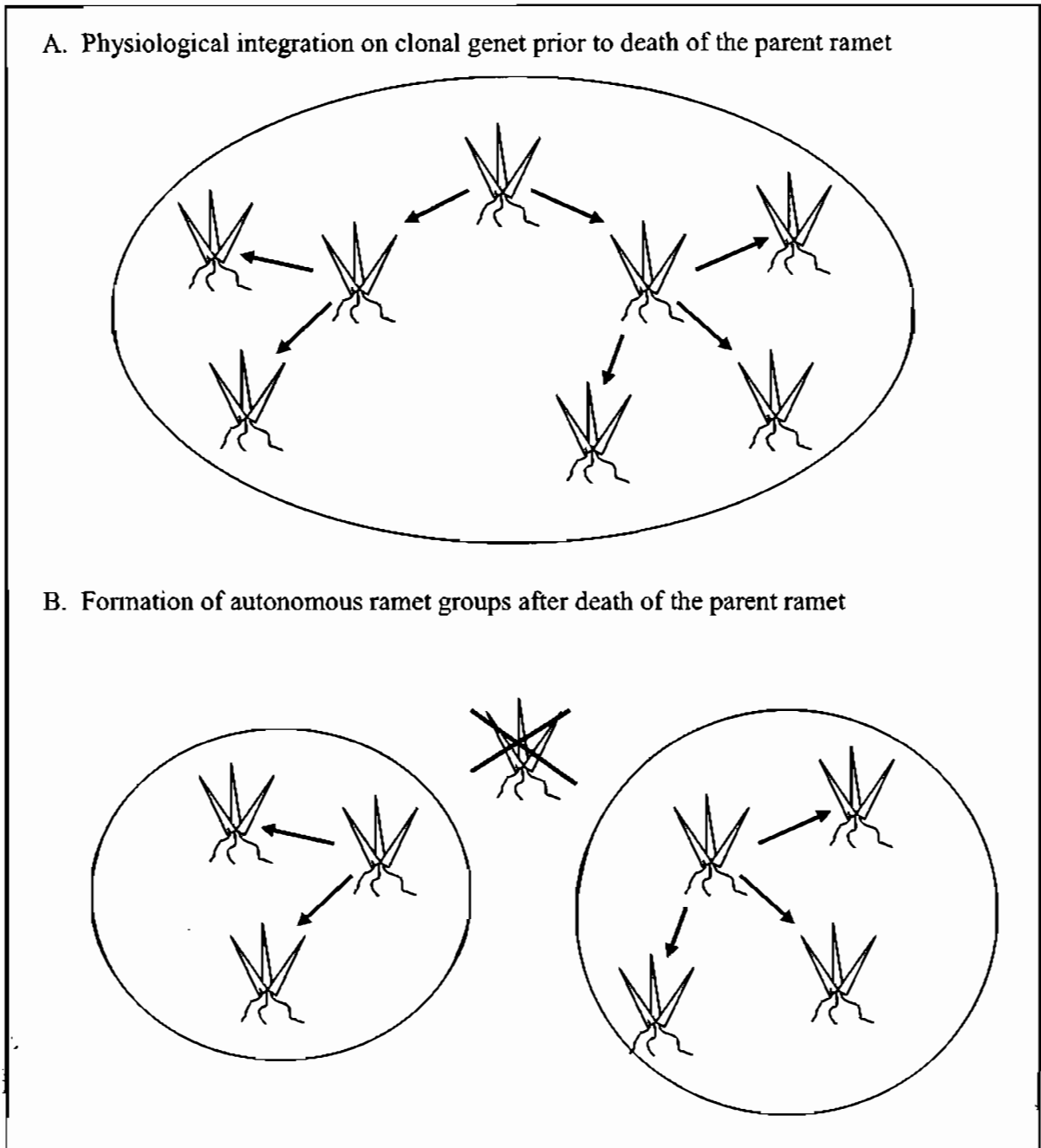
Figure 1.2 Physiological integration on a clonal genet before and after the death of a parent ramet. Ramets enclosed in the oval are physiologically connected to one another forming ramet groups. The arrows indicate the physiological connections from parent ramets to their daughters. Death of the parent ramet breaks the physiological connection between daughter sibling ramets, breaking the ramet group into a number of smaller ramet groups.

The existence of disconnected ramet groups on bunchgrass clones suggests that the benefits to the genet of physiological disintegration into smaller ramet groups appear to exceed the detrimental effects of competition among these ramet groups (Kelly 1995; Briske & Derner 1998).

2   LIMITING ENVIRONMENTAL RESOURCES IN HUMID GRASSLANDS

Growth in humid bunchgrass communities is limited by three main environmental resources, namely light, water and nitrogen, and restricted by a fourth environmental parameter, temperature (O'Connor & Bredenkamp 1997; Knapp *et al.* 1998). Knapp *et al.* (1998) proposed a non-equilibrium model for tall-grass prairie, a humid grassland type in North America in which growth is co-limited by light, water and nitrogen. These resources are dynamically variable and plant growth in any season is not continuous or linear, but rather it expresses as a series of growth pulses in direct response to events influencing the relative availability of the three limiting resources. Temperature is turn determines enzyme activity and therefore rates of growth in plants when resources are available.

2.1   Light and carbohydrates

Plants, as primary producers, are dependent on light to drive photosynthesis, the mechanism by which plants use photon energy to construct carbohydrates from carbon dioxide and water. Carbohydrates (CHO) are the basic building blocks for all structures in plants, and the energy source used by plants to drive chemical reactions. In addition carbohydrates may be stored by plants for use during periods when photosynthetic ability is restricted, either by the lack of photosynthetic organs or by environmental restriction of photosynthetic rate. Carbohydrates can be re-absorbed from plant structures for re-allocation in the plant. Therefore carbohydrates are a currency resource that can be manipulated by plants to adjust growth allocation.

Photosynthetic rate on any leaf surface depends in part on the quantity of light striking the surface. Light quantity is depleted as it passes through the leaf, thereby reducing the quantity of light available to photosynthetic leaf surfaces lower down in the canopy. Light is depleted exponentially as it passes down through an absorptive canopy (Beer's

Law). Both live and dead plant structures affect light penetration through a canopy. The intrinsic rate of light extinction varies in accordance with the angle and thickness of leaves in the canopy (Thornley & Johnson 1990). Therefore the vertical architecture of a plant has a direct bearing on its ability to capture light.

Bunchgrass species are especially vulnerable to light attenuation through their own canopies because of the manner in which they grow. Most bunchgrass species keep their tiller apical meristems close to the ground surface during non-reproductive growth, an adaptation presumably designed to protect the apical meristems from decapitation by defoliation. This means that new leaves must grow from the ground surface up through the canopy of surrounding leaves, which limits their photosynthetic ability until they approach the top of the canopy where light quantity is greater. In addition, individual leaves have limited life expectancy, so as dead plant matter increases in the canopy, light penetration through the canopy declines. Consequently self-shading within clonal bunchgrasses, caused by light attenuation through the tiller canopy, results in a reduction in potential carbon gains in these species (Ryel *et al.* 1994).

2.2 Nitrogen

Nitrogen (N) is a necessary component of proteins. Nitrogen deprivation limits the inclusion of carbohydrates into primary metabolic products necessary for plant growth and maintenance (Ariovich & Cresswell 1983) because it restricts the production of new protein molecules both in new growing organs and in existing organ cells where there is a rapid turnover rate of protein molecules (Penning de Vries 1975 cited by Amthor 1989). Actual nitrogen content in organs is variable, depending on the nitrogen absorption rate of the plant, the type of organ, the age of organs and their position in the canopy (Brown & Ashley 1974; Field 1983; Amthor 1989; Penning de Vries *et al.* 1989). Nitrogen is highly mobile in plants, and a large portion of nitrogen in organs is re-absorbed by plants for re-allocation (Friedrich & Huffaker 1980; Aerts 1996), and excess nitrogen appears to be stored in proteins (Huffaker & Miller 1978; Kang & Titus 1980; Moreno & Garcia-Martinez 1984; Quick *et al.* 1992). Therefore, like carbohydrate, nitrogen may be seen as currency resource that can be manipulated by plants to adjust growth allocation.

Plants obtain most nitrogen from the soil by root absorption. The availability of soil nitrogen to plants growing in humid grasslands is erratic and low, even though total soil

6

nitrogen can be substantial (Blair *et al.* 1998). Most available nitrogen in humid grasslands is stored in either plant or microbial biomass (Blair *et al.* 1998). Nitrogen that is released by decomposition of biomass is quickly immobilised by microbes and plants so it is only available to plants seasonally (Blair *et al.* 1998) and for short periods of time (Birch 1958). Generally nitrogen is available to plants in the form of short-duration flushes (Chapin 1980; Aerts & Chapin 2000). In humid grasslands nitrogen is added to the system by precipitation events. Burning the grassland also makes nitrogen available because some nitrogen is not re-absorbed during organ senescence and so nitrogen accumulates in non-decomposed dead plant matter. Net primary production after a fire is higher in tall-grass prairie that has not been burnt for a number of years than in annually-burnt prairie (Knapp *et al.* 1998). After a burn or precipitation event the available nitrogen in the soil quickly declines as most nitrogen gets absorbed by plants and microbes. The level of depletion by microbes depends on the carbohydrate-to-nitrogen ratio in the soil (Kaye & Hart 1997).

2.3   Soil water

Soil water is required by plants for growth and photosynthesis, and the rates at which these functions proceed are limited by transpiration rates in plants. Transpiration rate depends on water pressure differentials between the atmosphere and the soil. Plants can access soil water from the plant available water region, which generally lies between 0 kPa and −1500 kPa of soil water pressure, but plant cell turgor declines as the soil water pressure approaches the lower limit, which in turn reduces cellular activity and hence total plant activity. Water stress affects growth more acutely than photosynthesis. The plant process most susceptible to water stress appears to be cell growth, defined as the irreversible expansion of cells (Hsiao & Acevedo 1974). Maintenance respiration also declines in response to water stress, but too a much lesser degree than growth or photosynthesis (Wilson *et al.* 1980).

Local soil water is determined by precipitation inputs and evapotranspiration outputs and soil drainage movements (Schulze 1995). High evapotranspiration rates and intermittent rainfall events during the growing season in humid grasslands mean that soil water content is highly variable and is quickly depleted to levels that curtail plant growth in grassland communities (Woodward 1987; Schulze 1995; O'Connor & Bredenkamp 1997, Winslow, Hunt & Piper 2003).

There is little evidence to suggest that grasses store water actively. Rather their growth coincides directly with soil water availability, if other environmental factors are not inhibitive (Winslow *et al.* 2003). Therefore soil water pressure may be considered as an external environmental variable that moderates daily plant activity.

2.4 Temperature

Temperature determines the rate of chemical reactions in plants. Therefore it may be seen as an external environmental variable that moderates plant activity. Work summarised by Jones (1985) suggests that the relation between plant activity and temperature under optimal conditions (most particularly no water stress) is similar to most enzymatic reactions (Ludlow and Wilson 1971; Goudriaan and van Laar 1994), and follows a bell-shaped curve. There is a minimum temperature below which the plant tissues are inactive, a region of biological activity that increases to a maximum, after which activity decreases rapidly to a maximum temperature beyond which enzymes are denatured, leading to plant death.

Phenological development is accelerated by optimal temperatures and delayed by cooler temperatures. Tompsett (1976 cited by Jones 1985) observed that for the C_4 bunchgrass *Andropogon gayanus*, the time to anthesis decreases to less than half when mean temperature is raised from 17.5 °C to 27.5°C, the optimal temperature for the species. Within the growing temperature range of C_4 grasses, there appears to be minor variation across different processes. It appears that the temperature of the meristematic region of grass tillers determines the rate of tiller and leaf expansion, as long as the other plant parts remain within the growing temperature region (Watts 1974).

2.5 Growing and non-growing seasons

Air temperature (T) and soil water potential (Ψ_s) both act as environmental variables that moderate plant activity. That is, their effects limit the chemical reaction rates in plants, which in turn affect plant activity (Hsiao & Acevedo 1974; Jones 1985; Goudriaan and van Laar 1994). At any time in the year a non-growing period - a time interval when the surrounding environment is not conducive to active growth - is caused by inhibitively low

temperatures or inhibitively low soil moisture or both (Ellery, Scholes & Mentis 1991; Winslow *et al.* 2003).

Humid grasslands are usually characterised by a growing season and a non-growing season, where the non-growing season arises either from low temperatures or extended periods of low soil water (Ellery, Scholes & Mentis 1991; Winslow *et al.* 2003). The division of the annual cycle into a growing season and a non-growing season causes an extended period when no resources are captured. However leaves of bunchgrasses die back over the non-growing season which seriously reduces their photosynthetic capacity when growth commences at the start of the next growing season. For most bunchgrasses this environmental constraint is particularly serious because they are forced to recruit new blades from near the soil surface where their apical meristems are retained while they are not flowering. In addition the dead plant material decays slowly, so the new leaf blades are forced to grow through the overlying dead plant canopy to obtain light, which restricts their ability to overcome carbohydrate limitation. Clearly period of regrowth at the start of the growing season has the potential to be a severe resource bottleneck, indicating that the division of the annual cycle into growing and non-growing seasons is an important event affecting the growth of bunchgrasses.

3   GROWTH OF BUNCHGRASSES IN RESPONSE TO SPATIOTEMPORAL RESOURCE AVAILABILITY

Competition may be defined as the process by which plants capture and utilise limited resources at the expense of their neighbours. By this means they increase their own growth and suppress the growth of their neighbours. Competition between grasses may be considered from two perspectives (Lauenroth & Aguilera 1998): their competitive ability and their competitive response. Competitive ability can be evaluated in terms of the ability of an individual to suppress resources available to competitors. Competitive response is evaluated in terms of the ability of an individual to avoid being suppressed by responding to shifts in resource availability (Goldberg & Landa 1991). In this section I concentrate on structural adaptations used by bunchgrasses to respond to shifts in resource availability.

9

3.1 Light

Both canopy density and architecture influence the effect a plant will have on light interception. Grass species react differently to light quality, although few studies have attempted to order competitive responses of species or genets (e.g. Tremmel & Bazzaz 1993). An obvious source of differentiation is individual tiller and organ size. Clearly where competition for light is dominant, species that are taller have a competitive advantage, both because they can overshade their competitors thereby reducing the light reaching their competitors, and because they have the potential to overcome shading from competitors by growing above their competitors' canopy height. Most sun-grown plants also possess the ability to etiolate their leaves in shady conditions in order to increase their photosynthetic surface (Smith 1982). This property is potentially useful to grasses because it increases blade penetration up through the overlying canopy and therefore improves the plant's chances of sourcing better light quality (Casal, Sanchez & Deregibus 1985). Some species are also able to avoid self-shading by extending their internodes during vegetative growth (e.g. *Aristida junciformis*), but this makes them vulnerable to apical decapitation during the growing season, and their abundance declines relative to other bunchgrass species that do not possess this trait (e.g. *Themeda triandra*) under such conditions (Fynn *et al.* 2005a).

There is also evidence to suggest that bunchgrasses may respond to differences in light depletion across tufts through directed tiller recruitment: Greater tiller recruitment occurs on the edge than on the interior of bunchgrass tufts (Butler & Briske 1988; Olson & Richards 1988a), ostensibly because light competition is less intense on the edges than in the interiors of tufts. However this spatial tiller recruitment pattern persists after defoliation events that make the light environment more uniform (Olson & Richards 1988a), indicating that some other effect may be more overriding. Some species are also able to recruit aerial tillers on their reproductive culms, for example *Themeda triandra* and *Aristida junciformis* (Gibbs-Russell *et al.* 1990; Wolfson & Tainton 1999). This increases their access to direct sunlight and therefore increases photosynthetic production. Generally these aerial tillers are not long-lived in humid grasslands with established growing and non-growing seasons and they are killed by water limitations or frosting during the non-growing season (Wolfson & Tainton 1999).

3.2   Soil nutrients

Grasses are subject to strong competition for soil nutrients. Plants respond to spatiotemporal heterogeneity in nutrient distribution, both structurally by preferential proliferation of root and shoot systems in resource patches, and physiologically by elevation of uptake capacity (Drew, Saker & Ashley 1973; Eissenstat & Caldwell 1988a; Caldwell 1994; Hutchings & de Kroon 1994).

Nitrogen becomes available in humid grassland communities during short temporal pulses (Blair *et al.* 1998). It therefore seems likely that attributes promoting rapid uptake of nitrogen when it is available may promote species growth in nitrogen-limited environments (Campbell & Grime 1989; Tomlinson & O'Connor 2004). Species growing in nutrient-poor environments often have large root systems relative to their shoot systems with low root turnover, which promotes nitrogen absorption when it is available (Aerts & Chapin 2000). It is doubtful that this strategy is applicable to bunchgrasses because their growth strategy employs continual turnover of tillers and ramets that each have short life expectancy (less than two years; Tainton & Booysen 1965; Danckwerts 1984; Langer 1972; Briske & Richards 1995). Consequently, continued root persistence for longer than two years is improbable in caespitose species and doubtful in stoutly rhizomatous species. However this does not preclude the possibility that seasonal root growth patterns achieve similar results: soil nitrogen is most available during the start of the growing season. Therefore maintaining large root systems through the non-growing season on live ramets may promote nitrogen absorption at the start of the growing season.

Bunchgrasses recruit tillers in response to increased environmental nitrogen availability (Aspinall 1961; Laidlaw & Berrie 1974), indicating that tiller recruitment (shoot proliferation) is an important component of morphological plasticity in bunchgrasses employed during resource pulse periods (Briske & Derner 1998). We have proposed that this strategy increases the growth capability of bunchgrass clones during resource pulses, which increases their ability to accumulate nitrogen during these pulses (Tomlinson & O'Connor 2004).

Stoloniferous grasses are able to use shoot proliferation to search for nutrients across horizontally-heterogeneous resource environments, because of their horizontal stolon architecture (Hutchings & de Kroon 1994). Bunchgrasses do not possess this ability because their tillers grow upright so they can only move sideways as fast as they can recruit new tillers (Briske & Derner 1998). Soils under bunchgrass tufts have been found to have higher

11

organic carbon, organic nitrogen, net nitrogen mineralisation and respirable carbon compared with adjacent bare soil microsites (Vinton & Burke 1995), suggesting that they are able to accumulate nutrients from root foraging. This ensures that they are proximal to the nutrients stored in dead organic matter and therefore are able to absorb a greater fraction of these resources when they become available than surrounding competitors, indicating that responsiveness to temporal resource heterogeneity is critical in bunchgrasses.

3.3 Soil water

Grass species differ in their ability to deplete soil water in water limited environments, species with the ability to extract soil water to lower soil water pressures have a competitive advantage because they can continue to grow when their competitors are unable to do so. Highly competitive responses to water stress account for mechanisms of exclusion of native grasses by introduced African grasses in tropical savannas in Venezuela (Baruch & Fernandez 1993).

Soil water extraction ability depends on the size, number and spatial location of roots (Hook and Lauenroth 1994). Soil water uptake by plants requires that two conditions be met: a demand for water must be created by the physiological response of aboveground tissues, and the plant must have active roots in the wet soil. There is a trade-off for grasses between the amount of water gained and the carbon cost of producing new roots to access that water (Lauenroth *et al.* 1987). Differential responses of roots across soil layers may promote coexistence of species. There is some evidence that desert species increase root proliferation in response to water availability (Eissenstat & Caldwell 1988b), probably because it is such a limiting resources in these environments.

4 PLANT ARCHITECTURE AND DISPROPORTIONATE RESOURCE ALLOCATION

The evidence on the growth of bunchgrasses provided in the previous sections indicates that plants in general possess two key structural traits that define how they compete for resources in the environments they inhabit: architecture and disproportionate resource allocation to growth. The architectural constraints of plants define the limits within which

their growth response is confined (Herben & Suzuki 2002), for example organ morphology, location and number of meristems (Maschinski & Whitham 1989), and the development pattern of clones through tiller and ramet recruitment (Briske & Derner 1998). Plants allocate resources disproportionately and dynamically to increase the growth of particular plant structures at the expense of other structures within the confines of their architecture, in order to increase capture of resources distributed heterogeneously in the spatiotemporal environment they inhabit (de Kroon *et al.* 2005).

Disproportionate resource allocation can occur at a number of different levels in the hierarchy of clonal plants. At the highest level there may be disproportionate resource allocation among ramets within a ramet group which ensures plant growth proliferation in resource-rich spatial patches (Hutchings & de Kroon 1994; Briske & Derner 1998). Within individual ramets there is disproportionate allocation between the shoot and root which appears to be related to the relative supply rates of carbohydrate from the shoots and mineral nutrients from the roots (White 1937; Brouwer 1962; Andrews, Raven & Sprent 2001). This temporal adjustment of relative allocation to shoot and root on individual ramets is termed the "functional-equilibrium hypothesis" (Davidson 1969), now more commonly referred to as the "functional balance hypothesis" (Poorter & Nagel 2000). Within ramet shoots there may be disproportionate allocation among tillers (Bangerth 1989; Sachs, Novoplansky & Cohen 1993; Bangerth, Li & Gruber 2001) usually in response to the availability of light (Hutchings & de Kroon 1994). In ramet roots there is spatial branch proliferation in response to the distribution of soil nutrients (Caldwell *et al.* 1981). Finally there is priority in the allocation of resources between phytomers, such as the uneven distribution of nitrogen in leaves in plant canopies in response to the radiation environment within canopies (Friedrich & Huffacker 1980; Field 1983), and priority in allocation to phytomer organs (Reekie & Bazzaz 1987).

Although the effects of tiller-level and ramet-level structural properties on plant architectural forms are well understood (Woodward 1987; Prusinkiewicz & Lindenmayer 1990; Room et al. 1994; Briske & Derner 1998), little effort has been made to assess how interactions between disproportionate resource allocation and architecture affect the ability of plants to obtain and utilise spatiotemporally-heterogeneous environmental resources (Herben & Suzuki 2002). Understanding these interactions may identify critical features in the growth strategy of particular plant architectures that allow them to respond appropriately to resource heterogeneity. For example, bunchgrasses usually hold their tiller meristems close to the soil surface and recruit new tillers close to the soil surface, ostensibly to avoid

defoliation by fire or grazing. This architectural trait allows bunchgrasses to regrow rapidly after defoliation events. However it places them at risk of carbohydrate starvation caused by insufficient photosynthesis in non-defoliated swards. Therefore it is possible that dynamic disproportionate resource allocation combined with other structural adaptations may help plants overcome this problem.

All of the arguments provided so far point to the role of disproportionate allocation in improving resource capture in plants. An alternative function of disproportionate resource allocation may be to improve resource-use efficiency, by promoting the growth of fewer, more competitive structures. In other words population dynamics among structures on the clone may be critical to survival. In the case of clonal plants disproportionate allocation among ramets may ensure the survival of the largest ramets with access to the largest relative amounts of the most limiting resource that stand a better chance of survival during periods of severe environmental resource limitation. This behaviour may be especially true for perennial bunchgrasses because they are unable to spread sideways rapidly and therefore cannot search for soil resources across horizontal space. Rather they must make the best use of soil resources in the local horizontal space. However they must compete for local light in vertical space and local soil nutrients and survive periods of low resource availability, both within the growing season and across the non-growing season. By directing growth to fewer structures they may increase the growth of these structures and reduce the competition for resources from siblings during critical resource bottlenecks, thereby promoting the survival of the clone.

Further, interactions between properties at low levels of architecture and disproportionate resource allocation to discrete structures at higher levels of architecture (tillers, ramets) may change the ability of clones to accumulate particular resources thereby explaining competitive dominance among clonal species that have similar architectures at higher levels of hierarchy. For example shifts in organ structural parameters across bunchgrass species, such as organ growth rates and organ size, may change ability to compete for nitrogen and ability to compete for light thereby providing an alternative explanation for trade-offs between species with similar architectures along resource gradients (Tilman 1988) and defoliation gradients of grazing or burning (Belsky 1992; Grime 2001; Fynn *et al.* 2005a).

5   AIM AND OBJECTIVES

In order to understand how bunchgrasses achieve dominance over other plant types and how they achieve dominance over one another in different environments, it is first necessary to develop a detailed understanding of how their growth strategy interacts with the resource limits of their environment. In this thesis, I investigate the following question: How do interactions between architecture and disproportionate resource allocation in bunchgrass clones affect their ability to capture and utilise heterogeneous environmental resources?

The complexity of interactions among architecture, resource allocation and environmental resource dynamics are difficult to disentangle using empirical investigations as these are only able to collect information on direct relationships between dependent and independent variables. Mathematical simulation models are useful tools for studying multiple factors simultaneously in an integrated manner. Simulations models allow us to 'observe' the dynamic consequences of single properties or multiple interactions. However they are based on empirical evidence and many simplifying assumptions. Based on this we can use the simulations generated by the models to examine the consequences of our assumptions in the light of current knowledge.

The aim of this thesis is to use modelling as a tool to assess the consequences of interactions between architectural growth characteristics and disproportionate resource allocation at different levels of hierarchy of individual bunchgrass clones for their ability to capture and utilise environmental resources. In essence there are two distinct objectives:

1. Develop an appropriate model designed to consider the effects of interactions between bunchgrass architecture and resource capture and allocation on clonal growth and performance, measured in terms of clonal survival, population dynamics, resource capture, biomass production and biomass distribution (Chapters 2,3,4,5).

2. Use the model to investigate particular problems that involve interactions between architecture and disproportionate resource allocation in bunchgrasses. These shall include the following:

    (a) Adaptations used by bunchgrass ramets to gain access to light in closed swards (Chapter 6, Chapter 7).

    (b) Consequences of disproportionate allocation between ramets in ramet groups and tillers in ramets for clonal growth and performance, measured in terms of

clonal survival, population dynamics, resource capture, biomass production and biomass distribution (Chapter 8).

(c) Interactions between changes to phytomer-level parameters and disproportionate resource allocation between ramets and tillers, and its effect on clonal growth and performance (Chapter 9).

6   MODELLING APPROACH: AN INDIVIDUAL-BASED FUNCTIONAL-STRUCTURAL PLANT MODEL OF CLONAL GRASS GROWTH

The integration of physiology and architecture as aspects of plant function is the essential concept of functional-structural plant modelling (Sievänen et al. 2000; Allen, Prusinkiewicz & DeJong 2005). Surprisingly, a generalised plant functional-structural model has yet to be developed (de Reffye and Hu 2003). A recent integration of the L-systems 3-dimensional architecture model (Lindenmayer 1968) with a resource allocation model for trees, PEACH (Grossman & DeJong 1994), known as L-PEACH (Allen et al. 2005), may be the most advanced functional-structural model to date. Perennial growth across growing and non-growing seasons is a noted weakness in structural models with resource allocation (Le Roux et al. 2001). Therefore many functional-structural models are restricted to simulating growth within single seasons (Sequeira et al. 1991; Groot and Lantinga 2004). Most functional-structural plant models which do exist appear to be restricted to research on individual trees (Sequeira et al. 1991; Perttunen et al. 1996; Le Dizès et al. 1997; Allen et al. 2005) and ignore clonal ramet formation. Generally they are used for agricultural applications to forestry and horticulture and not for ecological questions such as competition and survival.

In order to model interactions between bunchgrass architecture and resource allocation and environmental resource dynamics, we seek a model that is explicit about individual organ growth on clones and about growth of individuals at the hierarchical levels already defined (phytomer, tiller, ramet, ramet group, clone).

Individual-based models allow one to simulate population behaviour as the sum of behaviours of individuals within that population as they react to environmental limitations and to other individuals in their local neighbourhoods. Hence populations can be studied at both the individual level and the population level (Judson 1994; Grimm 1999). In this sense a bunchgrass clone can be modelled as a population of individuals defined at different

hierarchical levels. In this manner clonal architecture is defined by the relationships between individuals both within and across the hierarchical levels. A number of recent architectural models have adopted this individual-based approach for studying clonal grasses (e.g. Groot & Lantinga 2004; Lafarge, Mazel & Hill 2005) using object-oriented programming.

In object-oriented programming (OOP), structures at each hierarchical level are treated as objects that have defined properties, both structural and physiological, associated with them. Objects communicate with one another via messages that invoke methods in other objects (Acock & Reynolds 1997). OOP uses the objects to make copies or 'instances' that run as individuals that are linked or unlinked to other instances in the program. This repeatability means that OOP is very useful for modelling individual-based populations where each individual can behave within some set of criteria defined for the object. Consequently behaviours of individuals (in our case phytomers, tillers, ramets, ramet groups) are simulated in response the environment and to neighbours, and population behaviour (in our case the bunchgrass clone) is the sum of the individual behaviours.

Architectural models may be spatially explicit in two dimensions (e.g. Groot and Lantinga 2004; Lafarge *et al.* 2005) or three dimensions (Lindenmayer 1968; Allen *et al.* 2005). Existing models of clonal plant growth can usually be divided into three groups, all of which are essentially 2-dimensional: The first group of models are explicit about vertical growth but not horizontal growth and include explicit resource allocation (Groot & Lantinga 2004). The second group are explicit about horizontal growth but not vertical growth, and do not include explicit resource allocation (Oborny 1994; Lafarge *et al.* 2005; Piqueras & Klimeš 1998). The third group are explicit or semi-explicit about horizontal growth but not vertical growth, but do incorporate explicit resource allocation (Herben and Suzuki 2002). The last group are designed to assess clonal growth and population dynamics in response to horizontal resource heterogeneity, but are of limited value for upright bunchgrasses because they ignore the vertical aspects of growth and therefore are unable to simulate photosynthetic limitation explicitly.

The model presented here, called the TILLERTREE model, is a 2-dimensional model that falls into the first group, in that it incorporates resource allocation, and treats vertical growth explicitly but ignores horizontal growth. The TILLERTREE model surpasses the model of Groot & Lantinga (2004) because it can simulate perennial plant growth across multiple seasons.

17

Presently the TILLERTREE ignores horizontal growth. This requirement was considered non-essential for the questions about bunchgrasses examined in this thesis, namely individual ramet responses to light limitation, population and growth responses of clones to disproportionate allocation at the hierarchical levels of tillers and ramets, and interactions between organ parameters and disproportionate allocation (see objectives, p 15). This is not to say that dynamics of bunchgrass clones are not affected by horizontal spatial dynamics. Certainly there are horizontal spatial effects across bunchgrass clones, such as tiller distribution (Butler & Briske 1988; Olson & Richards 1988 a,b). Rather, it is to say that temporal resource heterogeneity is probably more critical for population processes in bunchgrasses because they move horizontally very slowly and their growth strategy revolves around persistent site occupation (Briske & Derner 1998). In the future the TILLERTREE model will be extended to a 3-dimensional model in order to assess the relative importance of horizontal spatial effects to the growth of bunchgrass clones.

TILLERTREE simulates bunchgrass growth subject to production or capture and allocation of two resources that may be stored and re-allocated, namely carbohydrate and nitrogen. These two resources were identified as critical to the growth of bunchgrass clones in humid grasslands. Carbohydrate production is limited by photosynthesis, which is in turn limited by light distribution through the canopy. Nitrogen capture is limited by environmental availability in the soil and by root properties. Two other environmental factors affect daily growth activity, namely soil water availability and air temperature. These are treated as external parameters limiting daily plant activity.

7   MODEL PARAMETERISATION:
Themeda triandra AND THE SOUTHERN TALL GRASSVELD

This thesis seeks to explore the effects of interactions between architecture and resource allocation on growth of clonal bunchgrasses growing in humid grassland environments. Therefore it is necessary to parameterise the model for a species that occupies such an environment. The African C_4 caespitose bunchgrass species *Themeda triandra* is the most extensively researched bunchgrass in South Africa because it is a widely-spread species considered desirable for its forage value (Shackleton 1991). Local spring-flowering varieties of *Themeda triandra* have been extensively studied in the Southern Tall Grassveld, a humid grassland type dominated by bunchgrass species that is found in KwaZulu-Natal,

South Africa (Acocks 1953; Tainton & Booysen 1965; Fynn *et al.* 2005). Therefore *Themeda triandra* was chosen as the bunchgrass species simulated by the model throughout this thesis, and environmental data and characteristics for the simulations were based on a site in the Southern Tall Grassveld. This site is the Ukulinga Research Farm of the University of KwaZulu-Natal, in Pietermaritzburg. A full description of the site is provided in Appendix A1. Importantly the environment is characterised by a distinct growing and non-growing season, where the growing season extends from September to May each year

7   THESIS PRESENTATION

This thesis is divided into three sections. Section 1 provides a description of the model and its parameterisation. Sections 2 and 3 address particular questions on interactions between architecture and disproportionate resource allocation in bunchgrass clones.

In Section 1, the TILLERTREE model is presented in two separate chapters covering the two components of the model, namely structural growth (Chapter 2) and resource capture and allocation (Chapter 3). Model parameterisation for *Themeda triandra* and the Southern Tall Grassveld is provided in Chapter 4. Chapter 5 demonstrates the modelled growth of single ramets and provides validation to demonstrate that the model simulates tiller growth appropriately.

The architectural behaviour of bunchgrasses naturally divides into two components, namely the growth patterns of individual ramets, and the demographic patterns of interacting ramets in a clone. The growth patterns of individual ramets are of interest as these explain how individual shoots attempt to overcome light limitation. The demographic patterns of ramets indicate how clones respond to the interacting environmental constraints of light and nitrogen, and deals with issues of resource allocation among ramets and tillers that ensure optimal performance of the clone. Therefore the thesis is divided into a number of sections in order to deal appropriately with these two separate components.

Section 2 considers the growth of single ramets. Chapter 6 extends the model to allow for disproportionate allocation of resources between roots and shoots. Chapter 7 examines how individual ramets overcome the problem of light limitation during regrowth after the non-growing season.

Section 3 considers growth of multiple ramet clones. Chapter 8 considers the effect of disproportionate resource allocation among tillers and ramets on the growth of the clone,

19

the significance of clonal disintegration to clonal growth, and effects of tiller recruitment responsiveness to the two limited resources, nitrogen and light. Finally Chapter 9 examines the effect of specific organ characteristics on the abilities of bunchgrasses to capture and utilise nitrogen and carbohydrate.

The thesis ends with a synthesis of the bunchgrass behaviour observed with the model and indicates future research directions.

SECTION 1

The TILLERTREE Model

The first section of this thesis provides a description of the TILLERTREE model, which simulates the growth of individual bunchgrass clones. The model has been designed to consider the effects of interactions between bunchgrass architecture and resource capture and allocation on plant growth and performance, measured as short-, mid- and long-term survival, carbohydrate production, biomass production and biomass distribution. The model is composed using difference equations, and a discrete time interval of one day.

The model has two distinct components, namely structural architecture of an individual bunchgrass clone, and resource capture and allocation among structures on the clone. These are presented separately in Chapters 2 and 3 respectively. The model uses discrete object-oriented design in order to realistically mimic the architecture of clonal bunchgrasses. It includes a resource allocation model of two resources (nitrogen and carbon). The model description deliberately avoids reference to any particular species. This is in order to ensure that the model remains a generalised representation of growth in bunchgrass clones.

Chapter 4 provides parameterisation values for the species *Themeda triandra* and for the environment of the Southern Tall Grassveld. The final chapter in this section (Chapter 5) verifies that the model simulates the growth pattern of individual ramets appropriately, and validates the growth behaviour of individual tillers of *Themeda triandra* against empirical data.

Chapter 2:   Structural Growth in TILLERTREE

1   BUNCHGRASS MORPHOLOGY AND MODEL OBJECTS

The TILLERTREE model simulates the growth of individual bunchgrass clones. It considers plant objects defined at a number of hierarchical levels within a clone that have already been described in the Introduction (Figures 1.1 and 1.2), namely phytomers (a), tillers (β), ramets (γ), ramet groups (δ), and the clone itself (Figure 2.1).

Usually individual phytomers include the following organs: blade, sheath, and internode (Etter 1951; Kurihara et al. 1978; Bell 1991). In the TILLERTREE model flowers are also included in the phytomer structure because in many grass species flowers are borne on a number of phytomers near the terminal end of the tiller (Gibbs-Russell et al. 1990). Flowers are located on each phytomer at the distal end of each internode.

A tiller (β) consists of a number of phytomers connected sequentially to one another, with an apical meristem at its distal end that recruits new phytomers until the growth axis is terminated by flowering. Ramets are formed when tillers root. Ramets, which are functional plants containing shoot material and root material, may consist of several tillers connected to a single root system via the oldest parent tiller in the group. The simplest ramet consists of a single rooted tiller (known as a single-tiller ramet).

All ramets that are physiologically connected (termed physiological integration) in a ramet group are able to share nutrient resources. When the physiological connection between adjacent ramets is broken, connected ramets on either side of the broken connection form separate ramet groups (Figure 1.2). It seems likely that in most cases of caespitose grasses, ramets remain connected to their parent ramets as long as both are still alive (Danckwerts and Gordon 1987; Danckwerts and Gordon 1990; Briske and Derner 1998).In the model it is assumed that inter-ramet connectedness is broken by death of a parent ramet only (Figure 1.2).

Growth of the individual clone is recorded in the model in terms of the growth of individual organs (given the generic notation "o"). Four organ types are associated with each phytomer, namely blades (b), sheaths (s), internodes (in) and flowers (fl). Roots (r) are treated as the fifth organ type and are associated with each ramet (Figure 2.1). A description
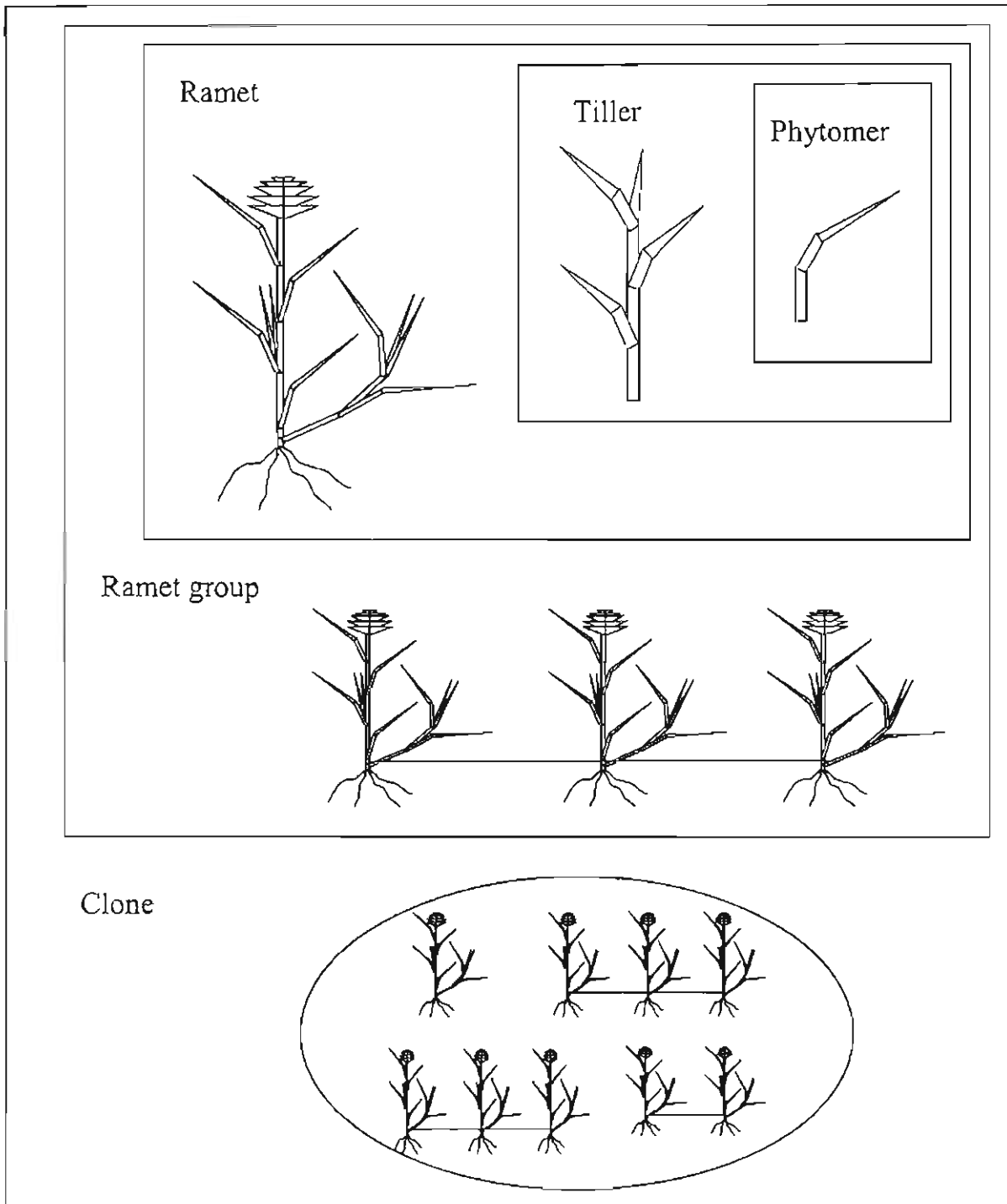
Figure 2.1 Object hierarchy of the architectural model of a bunchgrass clone as used by TILLERTREE. A phytomer is composed of the individual organs: blade, sheath, internode and flower. A tiller is composed of phytomers. A ramet is composed of a shoot system of connected tillers and a root system connected to the oldest parent tiller. A ramet group is composed of physiologically connected ramets. A clone consists of all disconnected ramets descended from an original seedling.

of how the growth of each organ type is simulated in TILLERTREE is provided in the sections that follow.

Subscript notation in the equations is designed to locate variables and parameters in the object hierarchy (α, β, γ, δ). In addition, i is used for parameters that may be species-specific. Time is represented by t in the usual manner. A further subscript, h, is used to denote height layer (described later). These subscripts locate the position and nature of each variable of each object in time and vertical space (variable$_{i,\alpha,\beta,\gamma,\delta,t}$). All calculations are made using a daily time step.

2 TILLER GROWTH

2.1 Tiller phenophase

Tillers pass through several stages of development during their life-cycles, known as phenophases. In this model, four possible phenophase states of tiller development are recognised.

Phenophase 1 (Vegetative phase):

> When a new tiller is initiated it enters Phenophase 1. The phenophase is characterised by leaf production, root production and marginal stem growth. A tiller will remain in Phenophase 1 until floral induction, unless it is prematurely apically decapitated, in which case it will enter Stasis (Phenophase 3).

Phenophase 2 (Sexual reproduction):

> This phase is characterised by leaf growth, stem expansion and flower growth.
>
> Floral induction is a species trait. It may depend on an environmental signal such as season (Opperman & Roberts 1978) or diurnal length (Blázquez & Weigel 2000). Alternatively it may be determined by a fixed number of phytomers from emergence to flowering.
>
> For the model, if a tiller shoot that is in Phenophase 1 and beyond a minimum age, enters the season of flowering, Phenophase 2 is induced. Floral induction is inhibited by the combination of low tiller mass and low resource reserves, which forces tillers into

Stasis (Phenophase 3). Alternatively, when flowering is complete, the tiller enters Stasis (Phenophase 3).

Phenophase 3 (Stasis):

When a tiller has completed flower growth or has had it apex removed by defoliation, it cannot proceed with further primary growth because it is no longer able to recruit any phytomers. If the tiller has dependent daughter tillers that do not have their own root system then the tiller is remains in Stasis in order to act as a resource conduit between these daughter tillers and the rest of the plant. The tiller will die back from the apex to the highest point along the stem at which a live daughter tiller is connected to it. As soon as the tiller has no live dependent secondary tillers, it is able to die back to its base and then dies itself, allowing it to proceed to Phenophase 4.

Phenophase 4 (Decay):

When a tiller dies, any live material is converted to dead material immediately and any remaining stored energy is also lost to the system. Decay proceeds on the dead tiller until all structural masses of the shoot have declined to zero, at which point the tiller ceases to exist as an entity in the system.

2.2   Tiller morphological types

Axillary bud development leads to quite different micro-environmental contexts for the initiated tillers and this in turn leads to the development of morphologically distinct tiller subtypes (Tainton & Booysen 1965). The TILLERTREE model recognises two basic morphological subtypes of grass tillers in tufted grass species, namely culm tillers and basal tillers. Culm tillers are initiated at axils of leaf nodes that are on that portion of the stem of the parent tiller that is expanded to elevate the flower head. As culm tillers are elevated substantially above the soil surface, they are unable to produce a root system and are unable to recruit secondary tillers.

Basal tillers are initiated at leaf nodes along the unexpanded portion of the parent tiller stem. Basal tillers have the potential to develop roots (but they may not do so) and are able to recruit secondary tillers.

3 PHYTOMER GROWTH

(Refer to Figure 2.2)

3.1 Phytomer organ growth phases

Plant growth characteristics in the phytomer object can be divided into those relating to each organ type on the phytomer. All phytomer organs go through the following series of life phases:

Organ Phase 1 (Expansion):

Active growth following initiation of the organ. The organ may proceed with functional activities (e.g. photosynthesis) during this phase.

Organ Phase 2 (Plateau):

Plateau period after growth is completed when the organ proceeds with its function.

Organ Phase 3 (Senescence):

Dieback of the organ after the plateau phase is completed. Some functions may slow down as the organ approaches death. Dead material begins to decay.

Organ Phase 4 (Decay):

Decay of dead organ matter. When this is complete the organ ceases to exist as a physical entity and is deleted in a similar fashion to tillers.

3.2 General difference equations for phytomer dimensions

Growth of an individual bunchgrass clone is the sum of growth of individual organs (blade, sheath, internode, flower) on that clone. Both length (mm) and dry mass (g DM) dimensions are recorded, and records are kept for live and dead material. Total material is calculated by summing the live and dead components. The state variables of each phytomer organ are live length ($llo_{\alpha,t}$), live mass ($wlo_{\alpha,t}$), dead length ($ldo_{\alpha,t}$) and dead mass ($wdo_{\alpha,t}$). Changes to organ mass are used to calculate the resource requirement for growth. Some organs increment their mass every cycle as they expand their girths, so mass values cannot be accurately predicted from lengths alone. For simplicity blades and sheaths are assumed
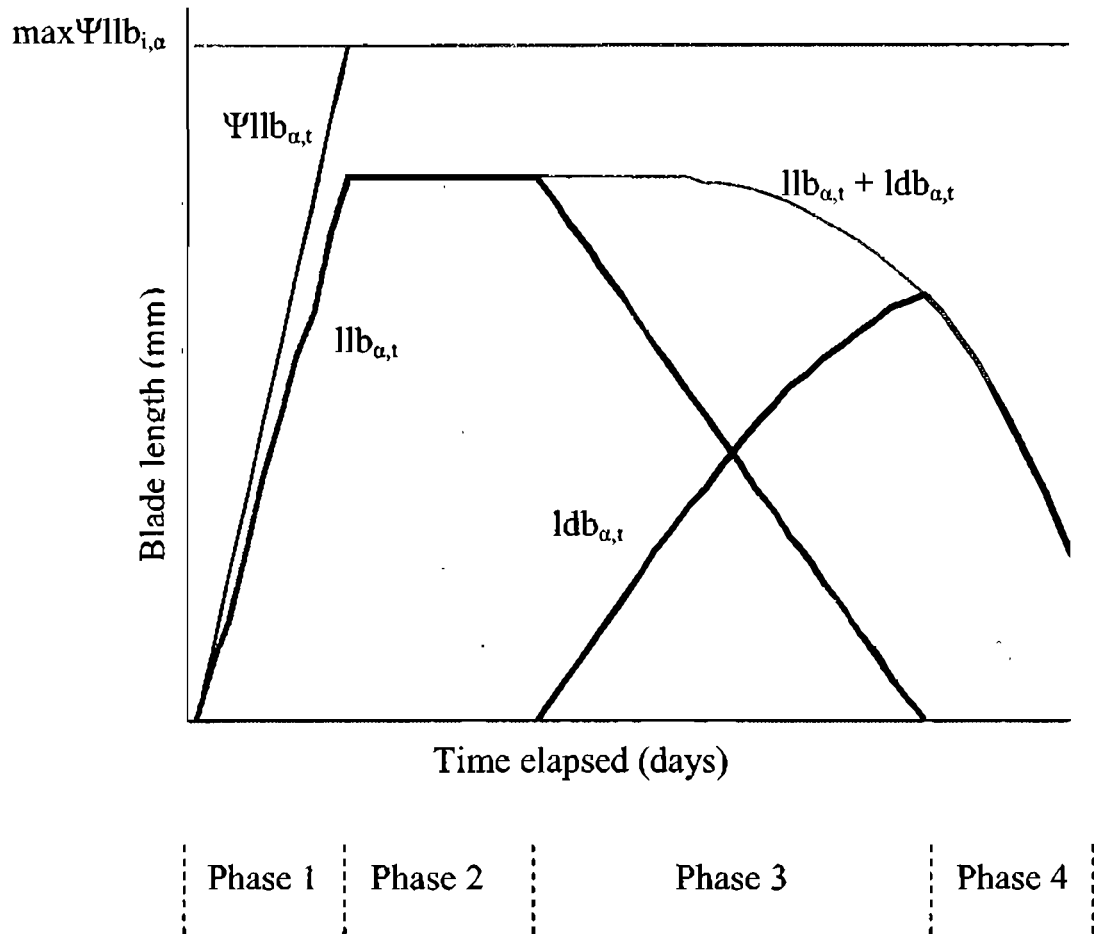
26

Figure 2.2   Growth phases of an individual blade organ (Phase 1: expansion; Phase 2: plateau; Phase 3: dieback; Phase 4: decay).

to be rectangular in dimension, internodes are cylindrical while flowers have no spatial dimensions. Flowers are only recorded in terms of their masses because they are usually sufficiently raised to be completely removed by any defoliation event, and it is assumed that they do not photosynthesise nor do they inhibit photosynthesis.

The live structure equations of individual organs on a particular phytomer contain growth ($gllo_{\alpha,t}$, $gwlo_{\alpha,t}$), dieback ($dllo_{\alpha,t}$, $dwlo_{\alpha,t}$), and defoliation ($cllo_{\alpha,t}$, $cwlo_{\alpha,t}$) components, while the dead structure equations have dieback, decay ($deldo_{\alpha,t}$, $dewdo_{\alpha,t}$) and defoliation components ($cldo_{\alpha,t}$, $cldo_{\alpha,t}$).

$$\Delta llo_{\alpha,t} = gllo_{\alpha,t} - dllo_{\alpha,t} - cllo_{\alpha,t} .$$ 2.1

$$\Delta wlo_{\alpha,t} = gwlo_{\alpha,t} - dwlo_{\alpha,t} - cwlo_{\alpha,t} .$$ 2.2

$$\Delta ldo_{\alpha,t} = dllo_{\alpha,t} - deldo_{\alpha,t} - cldo_{\alpha,t} .$$ 2.3

$$\Delta wdo_{\alpha,t} = dwlo_{\alpha,t} - dewdo_{\alpha,t} - cwdo_{\alpha,t} .$$ 2.4

3.2.1 Organ growth

Daily potential organ expansion ($\Psi gllo_{\alpha,t}$) is dependent on a maximum potential organ expansion rate ($\max\Psi gllo_i$), which is moderated by the environmental parameters average air temperature (T_{ave}) and soil water potential (Ψ_s) (e.g. Matthews et al. 1984 cited by Taiz and Zeiger 1998; Porter and Dellecolle 1988), and bounded by the maximum potential organ length ($\max\Psi llo_{i,\alpha}$), the maximum length that the organ can grow to under ideal conditions. As temperature and water restriction slow growth activity, these are assumed only to affect the time taken to achieve final organ size, and not to influence final organ size itself. A record is kept of potential organ length that would exist to date if resources were not restricted ($\Psi llo_{\alpha,t}$), in order to terminate growth of the organ when $\max\Psi gllo_{i,\alpha}$ has been attained.

$$\Psi gllo_{\alpha,t} = \min \left| \max \Psi gllo_i \min \left| f(T_{ave}); \ f_g(\Psi_s) \right|; \ (\max \Psi llo_{i,\alpha} - \Psi llo_{\alpha,t-1}) \right| .$$ 2.5

Maximum potential organ length ($\max\Psi llo_{i,\alpha}$) is a property of phytomer number, phenophase and species (Tomlinson & O'Connor 2005). During Phenophase 1 (Vegetative growth), leaf blades on early phytomers are short and consecutive phytomers have increased maximum potential blade length, until some maximum organ length for the species is achieved. Any more phytomers recruited during Phenophase 1 are assumed to have the same potential blade length. Blade lengths of phytomers recruited during the Sexual Reproduction Phase (Phenophase 2) become consecutively shorter (Table 4.1, Chapter 4). By contrast internodes on phytomers recruited during the Vegetative Phase are short, while internodes on phytomers recruited during the Sexual Reproduction Phase expand substantially to form the culm.

Potential organ mass growth is calculated from potential length and a live mass-to-length ratio ($awllo_i$), as there is a strong correlation between leaf dry mass and leaf length (Tainton & Booysen 1965).

$$\Psi gwlo_{\alpha,t} \quad = \quad awllo_i \ \Psi gllo_{\alpha,t} \ . \tag{2.6}$$

Actual daily organ expansion ($gllo_{\alpha,t}$) is limited by internal available resources (AllocatedAVC) and the growth conversion efficiency ($aCgo_i$), which is the amount of carbohydrate required per unit of mass growth. If the available resources are insufficient to meet the environmentally-limited growth requirements of the organ, the deficit in growth is treated as a permanent, non-recoverable loss that affects final organ size.

$$gllo_{\alpha,t} \quad = \quad \frac{\min\left[1.053 \ aCgo_i \ \Psi gwlo_{\alpha,t} \ ; \quad AllocatedAVC\right]}{1.053 \ aCgo_i \ \Psi gwlo_{\alpha,t}} \ . \tag{2.7}$$

Leaf sheath growth is subsequent to blade expansion on each phytomer (Kemp 1980; Skinner and Nelson 1994). Growth of internodes can be divided into two phases. There is marginal expansion on phytomers during Phenophase 1 and substantial expansion on phytomers recruited during Phenophase 2 (Tainton and Booysen 1965; Tomlinson and O'Connor 2005). Those internodes which expand are termed culm internodes, while the previous non-expanding internodes are termed basal internodes.

3.2.2   Organ senescence

Senescence on all organs proceeds from the distal end, from blade to sheath, at the maximal dieback rate $(\max\Psi dllo_i)$. Senescence rate depends on plant activity and is there subject to temperature.

$$dllo_{\alpha,t} \quad = \quad \max\Psi dllo_i \; f(T_{ave}) . \qquad\qquad \textbf{2.8}$$

Organ mass decreases when organs die because much of the cellular cytoplasm is re-absorbed (Penning de Vries *et al.* 1989). Therefore a conversion fraction, the organ proportional dead mass loss $(awdo_i)$, is used to calculate organ dry mass of dead organs after this reduction.

$$dwlo_{\alpha,t} \quad = \quad (1 - awdo_i)\, awllo_i \; dllo_{\alpha,t} . \qquad\qquad \textbf{2.9}$$

Senescence on leaves begins after each leaf has completed its plateau phase. Internode senescence is subject to three constraints. Firstly, the supported leaf sheath of the phytomer unit must have died back completely. Secondly, the adjacent superior internode must have died back completely. Thirdly, there must be no live tillers at the node of the phytomer. This structural order prevents the tiller stem dying back below nodes where there are dependent live tillers. Generally internode dieback is cued by Phenophase 3.

3.2.3   Organ decay

Decay of dead matter on all organs is simulated with an increasing exponential-type function (e.g. Deshmukh 1985). The function uses the maximum achieved length of the organ $(maxllo_{\alpha})$ and the actual length of the organ to calculate a gap on which the exponential change is calculated, in conjunction with an intrinsic decay rate $(Rdecay_i)$. The gap is initiated with an initial value of dead matter decay during the first cycle that the organ contains dead material (Gapinitialisor). Decay on organs proceeds from the distal end. Decay rate is assumed to be independent of temperature.

$$deldo_{\alpha,t} = (\max llo_\alpha)\, Rdecay_i \left[\frac{\max llo_\alpha - (llo_{\alpha,t} + ldo_{\alpha,t})}{\max llo_\alpha} \right].$$

$\qquad\qquad$ **2.10**

3.2.4 Organ defoliation

Live organ material may be removed by a defoliation event. A graze event is simulated in the TILLERTREE model as a vertical removal of plant material above a particular graze height. The model assumes that all phytomer organs are growing vertically. Therefore the height of a given phytomer organ can be calculated in terms of the lengths of all other internodes between it and the ground on its own tiller and any parent tillers on the same ramet. For example, defoliation of a blade organ on a particular phytomer on a particular ramet is as follows.

$$cllb_{\alpha,\beta,t} = gh - \left[llb_{\alpha,\beta,t} + lls_{\alpha,\beta,t} + \sum_{1}^{\alpha} llin_{\alpha,\beta,t} + \sum_{1}^{\beta-1}\sum_{1}^{\alpha} llin_{\alpha,\beta,t} \right].$$

$\qquad\qquad$ **2.11**

Because leaf blade meristems are located near the ligule at the base of the leaf blade, leaf blades are able to continue growth after defoliation events as long as the ligule meristem has not been removed. If the graze height falls below the ligule height of the phytomer, then the entire blade is removed together with its meristem and is therefore unable to grow again. If the graze height falls below the node height of the phytomer, then the entire leaf is removed. Removal of a node also removes the apical meristem of the associated tiller, thereby terminating growth on that tiller.

3.3 Individual flower mass

The live flower mass ($wlfl_{a,t}$) is able to increase exponentially to a maximum potential mass, but this maximum potential mass growth rate ($\max\Psi gwlo_i$) is limited by unfavourable environmental conditions in identical fashion to blades, sheaths and internodes. Once this is attained, the flower will stay in plateau for a period of time. This period is to allow for seed growth and setting. The flower then begins to die back at a rate proportional to its mass

(adlo$_i$). This senescence signals the completion of the tiller's sexual reproductive lifecycle. Dead flower mass decays in a similar fashion to other organs, except that mass values are used in the place of lengths.

3.4 Co-ordination of phytomer recruitment

Phytomer recruitment rate depends on species properties (e.g. Tainton & Booysen 1965; Appendix A1) and environmental factors (Nemoto, Morita & Baba 1995). It has been shown that there is co-ordination of growth between successive phytomers (Skinner & Nelson 1994). As sheath lengthening was completed on one phytomer, elongation of the associated axial bud began. At the same time the ligule was initiated on the next consecutive phytomer and blade lengthening began on the third phytomer in the sequence. Hence only two blades ever expanded at the same time. One direct consequence of this is that phytomer recruitment interval will lengthen or shorten in response to the blade length of the associated phytomer. Two main terms have been used to describe the interval between phytomer recruitments: the plastochron is defined as the interval between initiation of successive leaf primordia on the apical meristem, and the phyllochron is defined as the interval between consecutive similar visible developmental stages in phytomer growth (Wilhelm & McMaster 1995). In addition the environmental factors that have been shown to affect the phyllochron, notably temperature, daylength, nutrition, light intensity and humidity (see Nemoto et al. 1995) may be captured by their effects on growth of individual phytomer blades and sheaths.

The model uses this co-ordination property to determine phytomer recruitment. The model ignores the plastochron and cell division which directly follows phytomer initiation (Skinner & Nelson 1994), and concentrates on expansion events only in order to focus on linear growth behaviour as a matter of simplicity. Phytomer recruitment is defined in the following manner: once the potential blade growth on an existing phytomer has exceeded a certain fraction of the maximum potential growth (presently 90%), the next phytomer is recruited and begins blade expansion.

This phytomer co-ordination characteristic, if true for all grasses, means that the present model need only know the maximum blade expansion rates and the maximum length of organs of each phytomer of a grass species, as phytomer expansion interval will be determined by these properties.

4 ROOT GROWTH

Each ramet consists of a shoot and a root. Most research has focussed on the ontogenetic growth of above-ground plant parts, while the behaviour of root systems is not well understood because they are difficult to study. Usually all that is studied is root mass and the number of roots at any one time during the season (e.g. Tainton and Booysen 1965; Coughenour, McNaughton and Wallace 1985). It is probable that plants aim to maintain a functional balance ratio between shoot mass and root mass that relates to the relative rate at which each component supplies resources to the plant (Poorter and Nagel 2000).

In the model, roots are modelled in terms of mass only. Root growth and dieback depend on the root mass adjusting itself to stay in correct proportion with the shoot mass of the ramet. There is a goal-gap formulation between ideal root-to-shoot ratio, $\Omega alrlsh$, and actual root to shoot ratio (alrlsh, the ratio of root mass, $wlr_{\gamma,t}$, to shoot mass, $wlsh_{\gamma,t}$, which is the sum of live masses of all shoot organs on the ramet), which bounds daily root growth. Potential daily root growth ($\Psi gwlr_{\gamma,t}$) is also limited by the daily maximum root growth rate ($maxgwlr_{\gamma,t}$).

$$\Psi gwlr_{\gamma,t} = \min\left(\max gwlr_{\gamma,t} \ wlr_{\gamma,t-1}; \Omega alrlsh \ wlsh_{\gamma,t-1} - \frac{wlr_{\gamma,t-1}}{wlsh_{\gamma,t-1}}\right). \qquad \textbf{2.12}$$

The maximum potential daily root growth is scaled by the size of the existing live root system. At very small root sizes, daily root growth may equal existing total root mass due to the extension abilities of individual rootlets, if resources are available. However this relative growth rate of the root system rapidly declines as root mass increases. Therefore past a threshold root mass value of 0.1 g the maximum rate of root growth is fixed at a value of 0.05 g (g DM)$^{-1}$ d^{-1} (based on shoot growth rates from Wieners & Morris (2000).

$$\max gwlr_{\gamma,t} = \begin{cases} 1 - \dfrac{wlr_{\gamma,t-1}}{\left(0.1 - wlr_{\gamma,t-1}\right)}(1 - \max gwlr_i) & if \quad wlr_{\gamma,t-1} < 0.1, \\[2ex] \max gwlr_i & if \quad wlr_{\gamma,t-1} \geq 0.1 \ . \end{cases} \qquad \textbf{2.13}$$

Actual daily root growth ($gwlr_{\gamma,t}$) is determined by the resource availability.

$$gwlr_{\gamma,t} \;=\; \min\left(1.053 \; aCgo_i \; \Psi gwlr_{\gamma,t}; \quad AllocatedAVC\right). \qquad\qquad \textbf{2.14}$$

Root dieback depends on three things. Firstly, there is a background senescence rate that accounts for the natural turnover rate of live root material. Secondly, if defoliation causes the actual root-to-shoot ratio to exceed the $\Omega alrlsh_i$, roots will die back using the same value for maximum potential dieback as for maximum potential growth. Thirdly carbohydrate limitation may mean that there is insufficient carbohydrate for root maintenance. In this case, root dieback must increase up to maximum dieback rate to reduce the maintenance requirement and to free up carbohydrates to service the maintenance demand (described subsequently).

$$dwlr_{\gamma,t} \;=\; \max \left(\begin{array}{ll} 0.002 \, wlr_{\gamma,t-1} & , \\[2ex] \max dwlr_{\gamma,t} \; wlr_{\gamma,t-1} & if \quad \dfrac{wlr_{\gamma,t-1}}{wlsh_{\gamma,t-1}} \;\rangle\; alrlsh_i, \\[3ex] \max dwlr_{\gamma,t} \; wlr_{\gamma,t-1} & if \quad Cma\,int_{\gamma,t} \text{ not satisfied} \end{array} \right). \qquad \textbf{2.15}$$

5 COUNTER-TYPE STATE VARIABLES

In order to assess the structural behaviour it is necessary to keep summary records of live and dead objects at various levels in the system. These are termed counter variables. They are also state variables because they give the population sizes of live and dead objects on the clone on any given day.

Total live phytomer number ($l\alpha_t$) depends on recruitment and death rates and also on defoliation by grazing or fire events. Deaths rates are directly linked to the recruitment rate, with phytomer objects moving out of the system in response to the growth variables described above. Phytomers are also removed if a defoliation height to which they are subject falls below the height of the base height of their internode organ.

$$\Delta \sum l\alpha_t \;=\; \sum_\delta \sum_\gamma \sum_\beta \left[\sum_\alpha recruit_{\alpha,\beta,\gamma,\delta,t} \;-\; \sum_\alpha death_{\alpha,\beta,\gamma,\delta,t} \;-\; \sum_\alpha defoliated_{\alpha,\beta,\gamma,\delta,t} \right].$$

2.15

The number of tillers $(l\beta_t)$ depends on the recruitment rate of new tillers by the existing tillers on the ramet minus losses to tiller death and tiller defoliation.

$$\Delta \sum l\beta_t \;=\; \sum_\delta \sum_\gamma \left[\sum_\beta recruit_{\beta,\gamma,\delta,t} - \sum_\beta death_{\beta,\gamma,\delta,t} - \sum_\beta defoliated_{\beta,\gamma,\delta,t} \right].$$

2.16

Processes that govern tiller mortality are discussed subsequently (Section 4, Chapter 3). Tiller death may be due to ageing or it may be premature due to resource starvation. Tillers are also removed if the defoliation height to which they are subject falls below the basal height of their first phytomer.

The number of live ramets $(l\gamma_t)$ depends on the number of tillers that become rooted (breakoff) and on the death of ramets.

$$\Delta \sum l\gamma_t \;=\; \sum_\delta \left[\sum_\gamma \sum_\beta breakoff_{\beta,\gamma,\delta,t} \;-\; \sum_\gamma death_{\gamma,\delta,t} \right].$$

2.17

Death of ramets depends on the death of rooted tillers, the procedure for which is defined in the ordinary tiller death rules (Section 4, Chapter 3).

The number of live ramet groups at any given time is increased by ramet deaths, because this process breaks connections among live ramets (Figure 1.2), and is decreased by ramet group deaths. A ramet group dies when all ramets on that ramet group have died,

$$\Delta \sum l\delta_t \;=\; \sum_\delta \sum_\gamma death_{\gamma,\delta,t} \;-\; \sum_\delta death_{\delta,t}.$$

2.18

Chapter 3:   Resource Balance in TILLERTREE

Carbon (C) and nitrogen (N) are two of the most important resources in plant growth and their capture, sequestration and loss bound the growth behaviour exhibited by plants. Carbon is captured in photosynthesis and is converted into carbohydrates ($C_6H_{12}O_6$) while nitrogen is absorbed from the soil as NH_4^+. Carbohydrate is the building block for all structural components in the model as well as the fuel source providing energy to all endothermic chemical reactions within plants. Nitrogen is mainly used for construction of proteins, which control system functioning within cells. There are a number of other nutrients that are essential for plant growth, but these are ignored in order to ensure simplicity and also because their effect is probably largely over-ridden by the effects of nitrogen and carbon deprivation.

The chapter describes carbohydrate allocation first, followed by a discussion of nitrogen allocation and the points where the two components intersect in the model design. No attempt is made to incorporate ecosystem-wide carbon or nitrogen cycling. Rather, since the focus of this model is on the growth response of a grass plant to its given environment, environmental carbon and nitrogen are treated as inputs into the model.

A final section describes tiller mortality, which is determined both by structural and resource criteria.

1   CARBOHYDRATE

1.1   Concepts

1.1.1   Maintenance respiration and growth respiration

Non-structural carbohydrate provides the energy used for synthesis of new structures and renewal of existing structures. Therefore total respiration can be divided into two components: growth respiration is that respiration associated with the synthesis of new phytomass and maintenance respiration supplies energy to keep existing phytomass in a

35

healthy state (Amthor 1989). In general it is assumed that maintenance respiration takes priority over growth when soil water conditions are unfavourable for carbohydrate assimilation and cell expansion. However at a sub-cellular level, the two respiratory components cannot be separated since ATP energy for both components is derived from the same process: oxidation of glucose by the mitochondria. McCree (1982) measured maintenance coefficients of white clover at different growth rates. The coefficients varied from 2.4 mg CO_2 (g DM)$^{-1}$ h^{-1} down to 1.4 mg CO_2 (g DM)$^{-1}$ h^{-}l at zero growth, but the estimated value of growth conversion remained constant at 0.67 (720 mg CO_2 (g DM)$^{-1}$ grown). In other words maintenance respiration did decline as growth declined. This probably reflects the rate of protein turnover that is associated with cellular division and growth (Amthor 1989). Moser *et al.* (1982) found that tall fescue meristems can continue to grow for up to 16 days of darkness, providing additional evidence which suggests that maintenance respiration does not take full priority over growth. It would appear this is some form of sub-cellular control that regulates priority to maintenance processes over production of new structures, since maintenance is less affected by adverse environmental conditions such as water stress than growth (Wilson *et al.* 1980).

1.1.2 Reserve non-structural carbohydrates

Non-structural carbohydrate is divided into two components: ethanol-soluble material, which includes glucose, fructose and sucrose, and ethanol-non-soluble material, fructan and starch (Farrar & Williams 1991). Farrar & Williams (1991), working on non-structural carbohydrate concentration in roots of young barley plants, observed that total non-structural carbohydrate was about 70 − 100 mg (g DM)$^{-1}$, of which the ethanol solubles are half. They further noted that the soluble sugars were unevenly distributed in cellular tissues and that about 60 % of these sugars were compartmented into vacuoles. Farrar & Williams (1991) observed fluxes of sucrose into the root of 14 mg (g DM)$^{-1}$ h^{-1}, and that the vacuolar loading and unloading rate of soluble carbohydrate in response to shoot defoliation was fairly rapid at 5 mg (g DM)$^{-1}$ h^{-1}. By contrast there was little or only a slow change in the production or breakdown of starch polymers at 1.4 − 2.0 mg (g DM)$^{-1}$ h^{-1}. Douce *et al.* (1991) examined the autophagy in sycamore (*Acer pseudoplatanus*) cells subjected to sucrose deprivation. Notably starch mobilization only occurred after 10 hours of sucrose starvation, during which time the cells consumed most of the available soluble

carbohydrates. Therefore it is apparent that carbohydrates can be divided into two components, namely stored carbohydrates (starch and fructan), which are less available, and soluble carbohydrates (glucose, sucrose and fructose), which are more freely available for use in both growth and maintenance respiration.

The traditional role of stored carbohydrates in plant recovery following defoliation has been questioned (e.g. Wolfson 1999). This is because numerous researchers found a lack of clear correlation between non-structural carbohydrate concentrations (NSC, the traditionally perceived form of carbohydrate reserves in grass plants) and plant regrowth rates following defoliation. Richards & Caldwell (1985) suggested three reasons for this:

1. The contribution of photosynthesis from residual leaf material to regrowth is large relative to that of reserve substrates.

2. Non-structural carbohydrate reserves, as measured by traditional methods, do not adequately represent the available substrates for regrowth.

3. Meristematic restrictions resulting from the defoliation may limit regrowth more substantially than energy reserves.

Penning de Vries et al. (1989) note that much of the protein-rich cytosolic components are re-absorbed as plant tissues die, but none of the carbohydrate structures such as the cell walls are broken down. They estimated that about half of the cellular biomass of leaves may be re-absorbed, although they give no empirical backing for this estimate. The present model includes the ability to re-allocate carbohydrate as plant tissues senesce to account for this carbohydrate gain. It has been shown that grass species are differentially susceptible to defoliation because of their ontogenetic growth characteristics (Bridgens 1968; Caldwell et al. 1981; Coughenour et al. 1985).

The major storage region in grasses is the stem base, including underground stems in rhizomatous grass species (Wolfson & Tainton 1999), but stems and sheaths also contain major reserves of carbohydrates in some grass species (Richards 1984, Danckwerts & Gordon 1990). Roots have also been linked to carbohydrate storage in grasses (Nursery 1971).

The overall impression is that stored carbohydrate reserves are small and are used to initiate regrowth at any point in the season (Danckwerts 1984; Farrar & Williams 1991). As soon as active photosynthetic surface has been created, utilisation of stored carbohydrate

37

reserves begins to decline rapidly and soon switches to carbohydrate storage as supply rate exceeds demand rate (Farrar, Pollock & Gallagher 2000).

1.1.3 Seasonal patterns of reserve carbohydrate storage

Grasses require carbohydrate storage for two purposes: to provide energy for regrowth after defoliation events and to tide them over when environmental conditions are unfavourable for photosynthesis and growth. Tufted grasses of the Southern Tall Grassveld (Acocks 1953) apparently have a growing season from spring though to autumn, and a non-growing season during the unfavourable environmental conditions that prevail over winter every year. During the latter period, the grasses are unable to grow or photosynthesise appreciably because the temperatures are too cool and the soil is too dry for growth. Maintenance respiration continues at a much-reduced rate.

Reserve carbohydrate storage studies on native South African grasses in humid grasslands (Weinmann 1947; Weinmann 1948) and semi-arid grasslands (Danckwerts 1984) recorded maximum carbohydrate storage in mid-winter, strong depletion in spring and early summer and accumulation in autumn. Carbohydrate storage is generally at most about 10 % by plant tissue mass (Bartholomew 1968; Steinke & Booysen 1968; Danckwerts 1984; Farrar & Williams 1991).

The seasonal patterns of carbohydrate storage may reflect some seasonal strategy, but this explanation seems doubtful. An alternative explanation can be provided: there is a strong negative relationship between protein concentration and NSC concentration (e.g. Van Herwaarden, Richards & Angus 2003). Protein content reflects nitrogen (N) content, so it is probable that a plant's ability to use available carbohydrates is based on the availability of other resources. Consequently when nitrogen content is low, NSC is high and vice versa. In a subsequent section, nitrogen will be discussed more fully. However at this stage, it is pertinent to point out that nitrogen availability from the soil is highly seasonal and has rapid turnover periods (Blair et al. 1998), and is dependent on wetting and drying cycles (Birch 1958). Soil available nitrogen is high during early spring because it follows the longest period of low growth activity in a season.

1.2 The carbohydrate balance model

The model uses glucose as the currency of carbohydrate as good data exists relating glucose to photosynthesis, maintenance and growth (e.g. Penning de Vries et al. 1989). Non-structural carbohydrates are divided into two main components, available non-structural carbohydrates (AVC, which mimics ethanol-soluble compounds) and stored carbohydrates (Cstore, which mimics ethanol-insoluble compounds) that must first be deconstructed before they can be utilised for growth and maintenance. When a glucose unit is disconnected from the starch polymer, it becomes part of the AVC. Allocation to and from all components is made via the AVC.

Carbohydrate is supplied to the AVC from daily net photosynthesis ($CNetPs_{\gamma,t}$), and from re-absorption of structural materials when organs senesce ($Csenesce_{\gamma,t}$) (Penning de Vries et al. 1989). Growth ($Cgrow_{\gamma,t}$) and maintenance ($Cmaint_{\gamma,t}$) are both carbohydrate sinks. Carbohydrate storage ($Cstore_{\gamma,t}$) may act as a net sink or net source of resource depending on the ratio of carbohydrate demand to supply across the ramet (Fig. 3). Defoliation can also reduce non-structural carbohydrate ($cAVC_{\gamma,t}$) if live organ material is removed.

Carbohydrate may be shared with connected ramets on the same ramet group ($CRpool_{\gamma,\delta,t}$). Plants are only able to contain non-structural carbohydrate to a limited concentration. At the end of each iteration, the excess carbohydrate on this upper limit is converted to secondary metabolites ($CSecMetab_{\gamma,\delta,t}$) that is lost to the system.

$$
\begin{aligned}
\Delta AVC_{\gamma,t} = & \ CNetPs_{\gamma,t} + Csenesce_{\gamma,t} - Cma\operatorname{int}_{\gamma,t} - Cgrow_{\gamma,t} \\
& + \Delta Cstore_{\gamma,t} - cAVC_{\gamma,t} + CRpool_{\gamma,\delta,t} - CSecMetab_{\gamma,t} .
\end{aligned}
\qquad 3.1
$$

1.2.1 Photosynthesis

Phytomer blades, sheaths and internodes are all able to photosynthesise (Caldwell et al. 1981). The daily photosynthesis on an organ surface of a particular phytomer is dependent on the amount of light penetrating to that level in a canopy. Therefore the canopy is stratified into a series of canopy layers (h). The number and thickness of these layers is a user-defined property. Each phytomer organ is divided into segments of surface area (cm^2)

that correspond with each layer ($Alo_{\alpha,h,t}$). By this means values can be obtained for the overlying cnopy area for each layer (the leaf area index LAI), which is the sum of all live and dead blade and sheath material in overlying layers. Blades and sheaths are flat and so depend on the mass-to-area ratio ($awAo_i$), while internodes are cylindrical and so depend on density (pin_i).

$$Alb_{\alpha,h,t} = awllb_i \ llb_{\alpha,h,t} \left(\frac{1}{awAb_i} \right),$$

3.2

$$Alin_{\alpha,h,t} = 2\pi \ llin_{\alpha,h,t} \sqrt{\frac{wlin_{\alpha,h,t}}{pin_i \ \pi \ llin_{\alpha,h,t}}}.$$

3.3

Daily photosynthesis follows a model by Coughenour (1984). Maximum hourly photosynthetic rate per unit leaf area, $Pmax_i$ (g carbohydrate $cm^{-2} \ h^{-1}$), is the amount of carbon dioxide fixed per unit leaf area per hour. Photosynthetic rate is modified by the daily duration of sunlight (daylen), a constant 0.67 that accounts for the daily variation in light intensity (Coughenour 1984), light extinction in the overlying canopy ($F_p(LAI)$), and nitrogen concentration in the organ ($F_p(N)$). The constant 0.9 represents losses due to dark respiration (mg carbohydrate $dm^{-2} \ h^{-1}$), which are generally about 10% of gross photosynthesis (Herrmann & Schachtel 2000),

$$CNetPs_{y,t} = 0.9 \ Pmax_i \sum_\alpha \sum_h \left[\frac{Alo_{\alpha,h,t}}{100} F_p(LAI_h) F_p(N) 0.67 \ daylen \ F_p(oangle_i) \right]$$
$$* \min\left[f(T_{ave}); \ f_g(\Psi_s) \right].$$

3.4

$F_p(oangle_{i,\alpha})$ calculates the integral of daily light intensity at the organ surface as the product of the organ angle and the angle of the sun (sunangle) as it crosses the sky.

$$F_p(oangle_{i,\alpha}) = \int_0^\pi \sin(sunangle) \sin(|sunangle - oangle_i|) \ / \ \int_0^\pi \sin(sunangle).$$

3.5

Daily duration of sunlight (daylen) varies with latitude and day of the Gregorian year (Gregday) (Chidley & Pike 1970).

$$daylen = 12 + 2 \cos\left(\frac{2\pi(GregDay + 9)}{365}\right) + 0.22 .$$

3.6

Light extinction through the canopy is dependent on the extinction coefficient of the absorptive medium (K_i) in accordance with Beer's law (Goudriaan & Van Laar 1994).

$$F_p(LAI_h) = e^{-K_i * LAI_h} .$$

3.7

LAI_h in a particular height layer is the amount of light absorbing surface area in the canopy overlying that layer per unit area of ground surface (GSA), which consists of both live and dead blade and sheath material ($Ado_{\alpha,h,t}$) across all ramets in the modelled system.

$$LAI_h = \frac{1}{GSA} \sum_{h+1}\left[\sum_{\delta}\sum_{\gamma}\sum_{\beta}\sum_{\alpha}[Alo_{\alpha,h,t} + Ado_{\alpha,h,t}]\right] .$$

3.8

$F_p(N)$ is the effect of tissue protein content on photosynthetic rate (Leriche et al. 2001).

$$F_p(N) = 0.4107 + 0.1964\left(Nstore_{\gamma,t} + \frac{AVN_{\gamma,t}}{wltr_{\gamma,t}}\right) .$$

3.9

Photosynthesis may be restricted if intracellular carbohydrate content is high (Stitt et al. 1990) but the evidence is not consistent (Farrar et al. 2000). This is not applied in the current model.

1.2.2 Maintenance

Maintenance respiration is the daily carbohydrate required to maintain existing cells in each plant organ. Maintenance respiration is represented as a fractional cost of organ live mass ($Cmfrlo_i$), where individual organ types have different maintenance costs per unit mass

41

(Penning de Vries et al. 1989). An additional transport cost of 5.3 % by mass is associated with all carbohydrate allocations.

$$CMaint_{\gamma,t} = \left(\sum_{\beta} \left[\sum_{\alpha} 1.053 \; Cmfrlo_i \; wlo_{\alpha,\beta,\gamma,t} \right] + 1.053 \; Cmfrlr_i \; wlr_{\gamma,t} \right) f(T_{ave}). \qquad \textbf{3.10}$$

1.2.3 Growth

Structural growth is a large sink for non-structural carbohydrates. Growth respiration is the cost of carbohydrate for plant growth of all organs. The total growth demand of the ramet ($CDemGrow_{\gamma,t}$) is the sum of the growth demands of individual organs calculated from their growth rates and growth conversion efficiency ($aCgo_i$) and the additional transportation cost (Penning de Vries et al. 1989).

$$CDemGrow_{\gamma,t} = \sum_{\beta} \left[\sum_{\alpha} aCgo_i \; 1.053 \; \Psi gwlo_{\alpha,\beta,\gamma,t} \right] + aCgr_i \; 1.053 \; \Psi gwlr_{\gamma,t}. \qquad \textbf{3.11}$$

The estimated the cost of glucose for structural growth in rice crops is 1.326 g glucose $(g \; DM)^{-1}$ for leaves, stems and roots and 1.462 g glucose $(g \; DM)^{-1}$ for inflorescence and grain formation (Penning de Vries *et al.* 1989), which will be a sufficient approximation for the species under analysis.

1.2.4 Storage

Carbohydrate can be added to or removed from storage on any given day. Carbohydrate storage is a property of individual organs on individual phytomers. Daily storage movement across the ramet is the sum of movements within individual organs.

Storage movement is achieved in the model by utilising a gap-goal function where the actual value of carbon storage, $Cstore_{o,t,}$ aims for a daily ideal storage value. The level of $\Omega Cstore_{o,t}$, responds to the photosynthetic production of plants relative to their demands. In other words when demands are high and photosynthetic production is low, $\Omega Cstore_{o,t}$ is low

42

to allow more carbohydrate to be extracted from storage to feed these demands. When demands are zero, $\Omega Cstore_{o,t}$ is at the maximum value.

$$\Omega Cstore_{o,t} = \begin{cases} \max Cstore_{i,o} & if \quad CDemGrow_{\gamma,t} \leq 0, \\ \\ \min Cstore_{i,o} & if \quad NetPs_{\gamma,t} - Cma\operatorname{int}_{\gamma,t} < 0, \\ \\ \min Cstore_{i,o} + \left(\max Cstore_{i,o} - \min Cstore_{i,o}\right)\left(\dfrac{NetPs_{\gamma,t} - Cma\operatorname{int}_{\gamma,t}}{CDemGrow_{\gamma,t}}\right) \\ \\ \qquad otherwise. \end{cases} \qquad \textbf{3.12}$$

The rate of starch decomposition may depend on the starch type. Amylopectin is a multi-branched structure and therefore capable of constructing or deconstructing exponentially, whereas amylose is a single chain structure, which if this may not be spliced into smaller segments during disassembly would decompose at a more absolute rate. However it is apparent that starch splicing enzymes do occur (Whistler *et al.* 1984), so it is likely that decay is exponential. Therefore in each iteration, carbohydrate is supplied from storage ($CDemStore_{o,t}$) at a rate proportional to its mass, $RCstore_i$, to the AVC. After this amount is removed, a demand ($CDemStore_{o,t}$) is passed from $Cstore_{o,t}$, for carbohydrate storage, which is the minimum of two times the maximum transfer rate and the difference between actual storage and ideal storage. The net change in storage, $\Delta Cstore_{\gamma,t}$, is the summed difference between supply and demand across all organs.

$$CSupStore_{o,t} = RCstore_i \, Cstore_{o,t} . \qquad \textbf{3.13}$$

$$CDemStore_{o,t} = \min\left(2 * CDemStore_{o,t} \, ; |\, \Omega Cstore_{o,t} \, wlo_t - Cstore_{o,t} \,|\right). \qquad \textbf{3.14}$$

$$\Delta CStore_{\gamma,t} = \sum_{\beta}\sum_{\alpha}\left(CDemStore_{\alpha,t} - CSupStore_{\alpha,t}\right) + \left(CDemStore_{r,t} - CSupStore_{r,t}\right). \qquad \textbf{3.15}$$

Farrar & Williams (1991) measured starch breakdown rates of $1.4 - 2.0$ mg (g DM)$^{-1}$ h^{-1} in the roots of young barley plants, where the total amount of starch and fructan was $35 - 50$ mg glucose (g structural DM)$^{-1}$. Assuming that the starch decay rate is exponential, then the initial breakdown rate above yields an exponential decay rate of 0.041 g (g CHO)$^{-1}$ hr^{-1},

43

which means that up to 67 % of the stored carbohydrate may be mobilised in a day. However for the model it is assumed that the daily maximum rate of carbohydrate release from storage ($RCstore_i$) is assumed to be 0.1 times the amount of carbohydrate in storage.

1.2.5 Senescence

As individual organs senesce intra-cellular structures are decomposed, which provides carbohydrate and minerals for re-allocation. Penning de Vries et al. (1989) note that much of the protein-rich cytosolic components are re-absorbed as plant tissues die, but none of the carbohydrate structures such as the cell walls are broken down. They estimated that about half of the cellular biomass of leaves may be re-absorbed, although they give no empirical backing for this estimate. This seems very high and different organ types contain different levels of cytoplasmic material. Therefore the present model uses values of 0.1 by mass for blades and sheaths and 0.05 by mass for internodes, flowers and roots.

$$Csenesce_{\gamma,t} = \sum_{\beta} \sum_{\alpha} RCdieback_{i,o} \; dwlo_{\alpha,\beta,\gamma,t} + RCdieback_{i,o} \; dwlr_{\gamma,t} \; . \qquad 3.16$$

1.2.6 Defoliation

Defoliation of organ structures has already been described. Defoliation also removes non-structural carbohydrates that are housed in these organs. AVC is a property of the ramet. Therefore its depletion is calculated in direct proportion to the live mass of the ramet removed during the defoliation event relative to the total live mass of the ramet.

$$cAVC_{\gamma,t} = AVC_{\gamma,t} \left(\frac{\sum_{\beta} \sum_{\alpha} cwlo_{\alpha,\beta,\gamma,t}}{\sum_{\beta} \sum_{\alpha} wlo_{\alpha,\beta,\gamma,t}} + wlr_{\gamma,t} \right) . \qquad 3.17$$

$Cstore_{\alpha,t}$ is a property of individual organs, so depletion of stored carbohydrate by defoliation is also calculated in response to the proportional mass loss of each organ after a defoliation event.

$$\Delta Cstore_{\alpha,t} = -Cstore_{\alpha,t} \frac{cwlo_{\alpha,t}}{wlo_{\alpha,t}} . \qquad\qquad 3.18$$

1.2.7 Secondary metabolism

When carbohydrate production is high and nitrogen acquisition is below the required carbohydrate : nitrogen ratio of the plant, much of the carbohydrate is converted to secondary metabolites such as lignin and tannin. Secondary carbon compounds are produced by a ramet when the cellular concentration of non-structural carbohydrate (AVC) exceeds a certain critical value. This value is presently assumed to be 10 % by tiller mass, as this appears to be the upper limit on non-structural carbohydrate in the local C_4 grasses, both stored and free (Danckwerts 1984). Such excess may occur if the ramet is unable to utilise the carbohydrate synthesised by the ramet, either for growth or storage. Generally it is growth-limiting conditions that give rise to secondary metabolite production. Such conditions may arise either because carbohydrate production by the ramet exceeds the genetic growth potential of the ramet, or, more probably, actual growth is limited by environmental constraints, most notably nitrogen deprivation (Brown & Ashley 1874; Du Toit 1992). Evidence that nitrogen shortage is responsible for the accumulation of secondary compounds is supplied by Du Toit (1992) who found low tannin levels (65.4 mg (g DM)$^{-1}$) in *Eulalia villosa* when soil nitrogen levels were high (200 mg N (dm^3 soil)$^{-1}$ added) and high tannin levels (114.0 mg (g DM)$^{-1}$) when soil nitrogen was low (0 mg N (dm^3 soil)$^{-1}$ added).

Presently the model is only interested in plant growth and all direct effects that secondary metabolites might have on plant growth are ignored. Therefore the secondary metabolites are treated as an accumulation pool in each ramet and no effort is made to distribute the secondary metabolites among organ types. After carbohydrate and nitrogen have been assigned to all demands, if the remaining AVC exceeds 10% by live mass of the

45

entire ramet, then this excess is assigned to secondary metabolism. Consequently at the end of a day cycle the AVC cannot exceed 10% by mass of the ramet.

$$CSecMetab_{\gamma,t} = AVC_{\gamma,t} - 0.1*wltr_{\gamma,t} \qquad if \quad AVC_{\gamma,t} > 0.1*wltr_{\gamma,t}.$$ 3. 19

Thornley & Johnson (1990) present values for glucose requirement of the major secondary compounds, including values for lignins ranging from $1.770 - 1.867$ g glucose (g product)$^{-1}$, which indicates that they are able to absorb large amounts of excess carbohydrate.

2 NITROGEN

2.1 The necessity of nitrogen to plant growth

Nitrogen (N) is the most limiting nutrient to growth. Nitrogen is a necessary component of proteins. Nitrogen deprivation limits the inclusion of carbohydrates into primary metabolic products necessary for plant growth and maintenance (Ariovich & Cresswell 1983) because it restricts the production of new protein molecules both in new growing organs and in existing organ cells where there is a rapid turnover rate of protein molecules (Penning de Vries 1975 cited by Amthor 1989). Nitrogen constitutes 0.151 g N (g DM protein)$^{-1}$ of protein (Penning de Vries et al. 1989). It is estimated that on average proteins constitute 20% by mass of leaf DM and 8% by mass of stem, inflorescence and root (Penning de Vries et al. 1989). This converts to 0.0302 g N (g DM)$^{-1}$ for leaves and 0.0121 g N (g DM)$^{-1}$ for stem, inflorescence and roots respectively. Actual nitrogen content in leaves is variable, depending on the nitrogen absorption rate of the plant, the age of leaves and their position in the canopy (Brown & Ashley 1974; Jones et al. 1978 cited by Amthor 1989). For this thesis, these complications in nitrogen distribution in the plant are ignored. There is strong evidence that excess nitrogen is stored in proteins (Kang & Titus 1980; Moreno & Garcia-Martinez 1984), particularly in ribulose-1, 5-biphosphate carboxylase-oxygenase (RUBISCO) in leaves (Huffaker & Miller 1978; Quick et al. 1992).

2.2   The nitrogen balance model

The model uses a nitrogen economy that functions similarly to the carbon economy described above. The model contains two components of non-structural nitrogen that mirror the components of non-structural carbohydrate, namely available nitrogen (AVN), which is a ramet property, and stored nitrogen (Nstore), which is an organ property. All allocation of nitrogen both to storage pools and to growth is conducted through the AVN. In a similar fashion to the carbon economy, the nitrogen requirements (g N (g structural DM)$^{-1}$) of all organ growth is calculated by organ type. From this it is possible to determine for any particular day firstly whether or not nitrogen is limiting to growth in the plant system and secondly whether nitrogen is more limiting than available non-structural carbohydrate. Growth will then be instituted on the basis of the most limiting of the two resources in accordance with the growth demands placed by the organs.

Nitrogen is added to the AVN through root absorption of soil nitrogen (Nuptake$_{\gamma,t}$) and movement from storage (Nstore$_{\gamma,t}$). Nitrogen may also be obtained from re-absorption of structural materials when organs senesce (Nsenesce$_{\gamma,\delta,t}$) or are forced to dieback (Ndieback$_{\gamma,t}$) to supply carbohydrates to serve a maintenance deficit (Penning de Vries et al. 1989). There are two nitrogen sinks in the model, namely growth (Ngrow$_{\gamma,t}$) and storage (Nstore$_{\gamma,t}$). Non-bound nitrogen is subject to re-allocation across the ramet group (NRpool$_{\gamma,t}$) and to defoliation losses (cAVN$_{\gamma,t}$).

$$\Delta AVN_{\gamma,t} = Nuptake_{\gamma,t} + Nsenesce_{\gamma,t} + Ndieback_{\gamma,t} - Ngrow_{\gamma,t} \\ + \Delta Nstore_{\gamma,t} - cAVN_{\gamma,t} + NRpool_{\gamma,\delta,t} . \qquad 3.20$$

At this stage the assumption is made that no nitrogen is required for cellular maintenance as it is probable that almost all the nitrogen allocated to organs during their growth phases is re-allocated as proteins are made and destroyed.

2.2.1   Soil nitrogen uptake

Nitrogen absorbed through the roots is sent directly to the AVN. Nitrogen absorption depends on a maximum daily absorption rate per unit live root mass (Coughenour 1984). A

multiplier is included that reflects the daily availability of environmental nitrogen, which varies across a season (Blair et al. 1998). In addition, it is assumed that absorption of nitrogen per unit root mass decreases linearly as the density of live root mass increases relative to an upper limit on live root mass density (CCwlr). It states that the absorption of nitrogen decreases as the density of live root mass increases. Effects of temperature and soil water pressure on soil nitrogen absopriton are presently ignored.

$$Nuptake_{\gamma,t} = wlr_{\gamma,t} \ RNuptake \ mNuptake \left(1 - \frac{\displaystyle\sum_{\gamma}\sum_{\delta} wlr_{i,\gamma,\delta}}{CCwlr} \right).$$

3.21

Johnson & Thornley (1987) estimated that environmentally available nitrogen is absorbed from the soil at a rate of 0.05 g N (g root DM)$^{-1}$ d^{-1} (RNuptake$_i$). However a number of estimates from humid grasslands suggest that daily values absorbed from the soil are much lower. Coughenour et al. (1984) estimated daily absorption rates of 0.01-0.015 g N m^{-2} d^{-1} in the Serengeti. If it assumed that nitrogen is only available for four months of the year and a density of 1000 tillers m^{-2} (Coughenour et al. 1984), this converts to 0.00003-0.000045 g N tiller^{-1} d^{-1}. Values from the Konza Prairie experiments estimate yearly uptake at 4-5 g N m^{-2} yr^{-1} (Blair et al. 1998). This converts to approximately 0.000056 g N tiller^{-1} d^{-1}, which is comparable to the previous estimate of Coughenour et al. (1984).

Because nitrogen is actually only available in short pulses (Birch 1958, Blair et al. 1998), it is assumed that RNuptake$_i$ is intermediate between the estimate of Thornley & Johnson (1987) and the estimates of Coughenour et al. (1984) and Blair et al. (1998) at 0.001 g N (g root DM)$^{-1}$ d^{-1}.

2.2.2 Storage

Nitrogen is a highly limiting resource in humid grasslands that usually becomes available in flushes with long intermittent periods of low availability. It is probable that non-structural nitrogen is rapidly absorbed and hoarded by plants during these flushes (Aerts & Chapin 2000). Available evidence suggests that hoarded nitrogen is stored as protein (e.g. Huffaker and Miller 1978; Kang and Titus 1980; Quick et al. 1992). Nitrogen storage is an organ

property because there is some evidence that non-structural nitrogen is unevenly distributed among organs and organ types (Anten and Ackerly 2001). The nitrogen storage equations are identical to those for carbohydrate storage. As I have no data explicitly describing levels of nitrogen storage in plants, the ideal amount of storage per organ ($\Omega Nstore_{o,t}$) is assumed to be 1% for all organs (after Risser and Parton 1982). Nitrogen transfer rate to and from storage ($RNstore_i$) is fixed at 10% of $Nstore_{o,t}$ per iteration. The daily maximum rate of carbohydrate release from storage ($RNstore_i$) is assumed to be 0.1 times the amount of carbohydrate in storage.

2.2.3 Senescence

Senescence of leaf material (sheaths and blades), stem material and root material provides recycled nitrogen, which is returned to the AVN. The inflorescence is a sink for nitrogen that is entirely lost to the plant. The average estimate for nitrogen re-allocation ($RNdieback_{i,o}$) from senescent leaves in graminoids is 0.585 g g^{-1} N (Aerts 1996).

$$Ndieback_{\gamma,t} \;=\; \sum_{\beta} \sum_{\alpha} RNdieback_{i,o} * aNgo_i * dwlo_{\alpha,\beta,\gamma,t} \;+\; RNdieback_{i,r} * aNgr_i * dwlr_{\gamma,t} \; .$$

3.22

3 ALGORITHM FOR RESOURCE ALLOCATION

This section describes the procedural algorithm for resource movements within all objects on a bunchgrass clone during a single iteration.

1. Firstly carbohydrate and nitrogen additions from photosynthesis, soil nitrogen absorption, storage and senescence are added to the AVC and AVN pools of each ramet respectively. Secondly the demands for carbohydrate and nitrogen for growth, maintenance and storage in individual organs are passed to each ramet.

2. Following this all carbon and nitrogen in individual ramet AVCs and AVNs and total demands ($CDem_{\gamma,\delta,t}$) are passed to their parent ramet group. The ramet group supplies resources back to the ramets in proportion to their demands ($CSupDem_{\delta,t}$). If there are excess resources in the ramet group after the demands have been supplied ($CExcess_{\delta,t}$) then the remaining carbohydrate in the ramet group is allocated back to the ramets in proportion with their shoot masses. Therefore the net change in carbohydrate in the AVC of a given ramet on a given day ($CRpool_{\gamma,\delta,t}$) is equal to the difference between the amount of carbohydrate that has been supplied back to the ramet by the ramet group and the amount in the AVC before it was passed up to the ramet group.

$$CRpool_{\gamma,\delta,t} = CSupDem_{\delta,t} \frac{CDem_{\gamma,\delta,t}}{\displaystyle\sum_\gamma CDem_{\gamma,\delta,t}} + CExcess_{\delta,t} \frac{wl\gamma_{\gamma,\delta,t}}{\displaystyle\sum_\gamma wl\gamma_{\gamma,\delta,t}} - AVC_{\gamma,\delta,t}.$$

$$3.23$$

The procedure is identical for nitrogen allocation to idnvidual ramets in the ramet group.

3. After resources have been reassigned to individual ramets, allocation to organs proceeds in the following manner: First carbohydrate maintenance demands are supplied, then carbohydrate storage demands, and then growth demands are supplied. The separation and prioritization of maintenance over growth allocation is a reasonable assumption for models and is generally used (Coughenour 1984; Sequeira et al. 1991). Insertion of allocation to storage before growth ensures more conservative behaviour. This model assumption may be reviewed in future research because there is evidence that reserve carbohydrate storage is inversely related to the nitrogen status of a plant (Oparka et al. 1986), and therefore of lower priority than growth.

50

4. If there is insufficient carbohydrate in an iteration to satisfy the maintenance demand, the ramet is forced to dieback leaf and root material to satisfy the respective deficits of shoots and roots. Leaf material is senesced from the distal end, in identical fashion to programmed senescence. This dieback proceeds at the maximum dieback rate, and begins on the oldest live leaves first. Root dieback also proceeds at the maximum rate.

5. Allocation to growth within ramets is limited by the more restricted resource of nitrogen and carbohydrate. This is the point of interaction between the two models, and reflects the stoichiometric relationship between the growth requirements for the two resources.

$$
Cgrow_{\gamma,t} = \begin{cases} CDemGrow_{\gamma,t} & if \quad \left[(AVN_{\gamma,t} \geq NDemGrow_{\gamma,t}) \cap (AVC_{\gamma,t} \geq CDemGrow_{\gamma,t})\right], \\[2em] CDemGrow_{\gamma,t} \dfrac{AVN_{\gamma,t}}{NDemGrow_{\gamma,t}} & \\ & if \quad \left[(AVN_{\gamma,t} < NDemGrow_{\gamma,t}) \cap (AVC_{\gamma,\delta,t} \geq CDemGrow_{\gamma,t})\right], \\[2em] AVC_{\gamma,\delta,t} & if \quad \left[(AVN_{\gamma,t} \geq NDemGrow_{\gamma,t}) \cap (AVC_{\gamma,\delta,t} < CDemGrow_{\gamma,t})\right], \\[2em] CDemGrow_{\gamma,t} \min\left(\dfrac{AVN_{\gamma,t}}{NDemGrow_{\gamma,t}} ; \dfrac{AVC_{\gamma,t}}{CDemGrow_{\gamma,t}}\right) & otherwise. \end{cases}
$$

3.24

6. Once total resource-limited growth carbohydrate has been calculated for each ramet, this is divided between the root and shoot on that ramet. Subsequently, the resource assigned to each ramet shoot is divided among the connected tillers, and then divided among the phytomers on each tiller. Finally the growth resource assigned to each phytomer is allocated to its component organs.

7. Secondary tiller recruitment is attempted on the basis of resource availability (described subsequently) after primary growth allocation.

8. Finally at the end of the iteration, nitrogen is allocated to storage, and if carbohydrate in AVC exceeds the maximum allowable carbohydrate concentration, the excess is converted to secondary metabolite and removed from the system.

4   TILLER MORTALITY

Tiller mortality can be classed into two types. A grass tiller may die after completing its life-cycle (flowering and seeding), as often occurs in annual species. This is termed programmed senescence. Alternatively a tiller may be killed prematurely by unfavourable environmental conditions. This is termed premature termination. During favourable environmental conditions, an individual tiller of a perennial grass species does not necessarily die on completion of seed set. If it is linking other live tillers to a root system, then the stem portion of that tiller will continue to live as long as its dependent tillers are still alive. It is probable that there is some ageing process which limits the lifespan of individual tillers (Everson, Everson & Tainton 1985), perhaps based on some reduced efficiency of the conduits in the stem and roots. However this process is not understood and it is not considered.

In the model tiller death is induced by resource carbohydrate starvation combined with an inability to overcome this resource deficit in the near future. This is characterised by both a lack of sufficient stored reserves and a photosynthetic rate that is insufficient to supply maintenance demands and is therefore unable to supply any carbohydrate for growth. Since maintenance demands are determined by the size of the plant, induced dieback of the plant could provide a twofold benefit to overcome resource restriction, by firstly reducing the maintenance demand and secondly providing some additional non-structural carbohydrate from cellular deconstruction. Therefore a size constraint must be placed over plant death that ensures that tillers have died back substantially before they are terminated. These rules are sufficient to cover both premature termination and programmed senescence.

Tillers and even whole tufts are often killed during extended drought periods (Danckwerts & Stuart-Hill 1988; O'Connor 1994). However grass tillers appear to survive dry conditions during winter in the humid grasslands of Natal (Tainton & Booysen 1965). The reason for this dichotomy may be explained in the following manner. Most C_4 grasses lack true dormancy. Rather tiller growth rate and photosynthesis are restricted by environmental limitation due to both ambient temperatures and soil water pressure. Importantly chemical reaction rate is mainly determined by temperature. This means that maintenance demands during dry periods may be relatively large if temperatures are high even if there is no potential for growth and no potential to photosynthesise, thereby depleting stored reserves rapidly. In contrast low temperatures in winter slow chemical reaction rates almost to zero, thus slowing resource depletion substantially. Therefore water

52

stress induces carbohydrate exhaustion of tillers when ambient temperatures are high. Consequently water stress is not included directly in the rules for mortality.

4.1 Model rules for tiller mortality

In the model tiller death is induced by resource carbohydrate starvation combined with an inability to overcome this resource deficit in the near future. This is characterised by a lack of sufficient stored reserves, a photosynthetic rate that is insufficient to supply maintenance demands and is therefore unable to supply any carbohydrate for growth, and a size constraint that ensures that tillers have died back substantially relative to a maximum live mass ($Maxwl\beta_{\beta,t}$) before they are terminated and therefore are unable to supply resources from additional dieback.

$Phenophase = 4$ if

$$\left(\frac{wl\beta_{\beta,t}}{Maxwl\beta_{\beta,t}} < 0.1\right) \cap \left(\frac{CMa\operatorname{int}_{\beta,\gamma,t}}{CNetPs_{\beta,\gamma,t}} < 1\right) \cap \left(\frac{\sum_{\alpha} Cstore_{o,\alpha,\beta,t}}{wl\beta_{\beta,t}} < 0.001\right) \cap \left(AVC_{\gamma,t} \leq 0\right).$$

3.25

In addition, the tiller must have no dependent secondary tillers. This means that tiller death will always occur from daughter tillers to parent tillers. If the tiller that dies is directly connected to the root system, then this also kills the ramet. The tiller must be older than 15 days to prevent immediate termination due to small size if growth is initially slow.

Tillers may also be killed by sudden events such as complete removal by grazing or fire, and death by freezing during winter. Complete removal occurs if the defoliation event cuts the tiller below its base. Subzero temperatures kill all leaves but protected, unexpanded apical meristems are left intact if these are below some critical height. Tillers whose apical meristems are above the critical height are terminated but not killed, while those whose bases are above the critical height are killed.

Chapter 4:   Model Parameterisation

The model was parameterised to simulate growth of the spring-flowering African C_4 caespitose bunchgrass species *Themeda triandra*. *Themeda triandra* is the most extensively researched bunchgrass in South Africa because it is a widely-spread species considered desirable for its forage value (Shackleton 1991). Therefore *Themeda triandra* was chosen as the base species to parameterise the model and is used for all the simulations in this thesis.

1   STRUCTURAL ORGAN PARAMETERS

Structural growth of bunchgrasses is simulated by the TILLERTREE model by simulating the growth of individual organs. Therefore species-specific data was required for individual organs in order to simulate growth of the considered species realistically. Although there was a substantial body of research on the autecology of *Themeda triandra*, more data was required on the growth characteristics of individual organs. Therefore a number of simple field investigations were conducted in order to provide organ parameter values for the model. These investigations are presented in Appendix A1.

Maximum potential organ lengths (maxΨllo$_{i,a}$) are a characteristic of individual phytomers, so data was required for these parameters at the individual phytomer level. Phytomer-level data for *Themeda triandra* tillers growing in the Southern Tall Grassveld was collected by Wieners & Morris (2000 unpublished data) on the Burn-Mow Trial at Ukulinga Research Farm in Pietermaritzburg for the vegetative phase of growth (see Appendix A1 for a description of the Burn-Mow Trial experiment). Additional data was collected from the Burn-Mow Trial to parameterize maximum potential organ lengths for the Reproductive Growth Phase, for growth under light-limited and non-light-limited conditions. This was done by collecting data from treatments that were defoliated and not defoliated prior to spring regrowth and flowering. Other structural parameters were also collected and these trials are presented in Appendix A1. The parameter estimates for the structural model are presented in Tables 4.1 and 4.2. Data for *Themeda triandra* was also available from the work of Coughenour *et al.* 1984 in the Serengeti, East Africa.

54

Table 4.1 Maximum potential organ lengths ($\max\Psi$llo$_{i,a}$) for blades, sheaths and internodes, and maximum flower mass ($\max\Psi$wlf$_{i,a}$) for individual phytomers of *Themeda triandra*. Sexual reproductive phase data includes organ growth on treatments with a late winter defoliation and without defoliation (in paranthesis) (sources: Tomlinson and O'Connor 2005; Wieners and Morris 2000)

Phytomer	Organ type			
	Blade (mm)	Sheath (mm)	Internode (mm)	Flower (g)
Vegetative phase				
1	26.03	15.0	1.0 / 10.0*	
2	65.43	18.0	1.0 / 10.0	
3	70.4	25.0	1.0 / 10.0	
4	83.7	28.0	1.0 / 10.0	
5	99.0	32.0	1.0 / 10.0	
6	107.34	34.0	1.0 / 10.0	
7	151.81	50.2	1.0 / 10.0	
8	15.37	60.0	1.0 / 10.0	
9	213.87	70.0	1.0 / 10.0	
10	260.08	75.0	1.0 / 10.0	
11	277.34	75.0	1.0 / 10.0	
12	341.0	75.0	1.0 / 10.0	
13	427.5	75.0	1.0 / 10.0	
Sexual reproductive phase				
1	100.0 (241.0)	49.0 (72.0)	13.0 (138.0)	
2	102.5 (170.0)	48.8 (72.0)	24.0 (235.0)	
3	109.4 (153.0)	57.5 (58.0)	86.5 (270.0)	
4	118.0 (108.0)	54.0 (58.0)	204.0 (225.0)	0.03
5	84.4 (58.0)	41.0 (51.0)	235.0 (135.0)	0.03
6	50.8 (46.4)	28.0 (28.0)	151.0 (100.0)	0.03

* The length of vegetative internodes, depends on whether they are recruited before (1 mm) or after (10 mm) 1 January each year, after Tainton & Booysen 1965

Table 4.2 Structural parameter estimates used in the model as defined for the bunchgrass species *Themeda triandra* (sources of estimates are cited)

PARAMETER*	ORGAN					SOURCE
	Blade	**Sheath**	**Internode**	**Flower**	**Root**	
Mass relationships						
awllo$_i$	0.000172	0.000197	0.000205			Appendix A1
minawllo$_i$	0.000052					Appendix A1
maxawllo$_i$	0.000172					Appendix A1
awAo$_i$	0.004053	0.004437				Appendix A1; Coughenour *et al.* 1984
po$_i$			0.000254			Appendix A1
Growth						
maxΨgllo$_i$	12.5	12.5	12.5			Appendix A1
awlo$_i$			0.0183			Appendix A1
maxΨgwlo$_i$				0.05	0.05	Assumed
minalrlsh$_i$					0.5	Webb 2004
maxalrlsh$_i$					1.8	Webb 2004
Dieback						
Organ plateau length	34			21		Appendix A1
maxΨdllo$_{i,j,k}$	12.5	12.5	20.0			Tomlinson 2005
awdo$_i$	0.1	0.1	0.05	0.05	0.05	Assumed
adlo$_i$				0.1		Assumed
Root normal dieback					0.002	Assumed
Max root dieback					0.05	Assumed
Decay						
Difference initialisor	1mm	1mm	1mm	0.01 g	-	Assumed
Rdecay	0.012	0.012	0.012	0.012	-	Assumed based on simulations

2   RESOURCE ALLOCATION PARAMETERS

Estimates for resource allocation parameters were chosen from generic estimates for C_4 species, largely taken from Penning de Vries *et al.* (1989) (Table 4.3). Where specific estimates for *Themeda triandra* existed, these were used.

3   ENVIRONMENTAL NITROGEN

Photosynthetic production depends on the architecture of the bunchgrass clone as described in the previous chapter, and is restricted by temperature and soil water potential. Nitrogen capture depends on root mass and environmental soil nitrogen availability that is imposed externally in the TILLERTREE model.

Although seasonal movements in soil nitrogen availability in humid grasslands are understood (e.g. Blair et al. 1998), actual daily amounts of nitrogen available to be absorbed by plants are more difficult to quantify as these appear to change rather rapidly (Birch 1958). Nitrogen appears to become available in pulsed flushes following burning or rainfall events (Blair et al. 1998; Knapp et al. 1998). After a burn or thunderstorm activity the available nitrogen in the soil rises rapidly and then quickly declines as most nitrogen gets immobilised into microbial biomass or is absorbed by plants, depending on the carbohydrate-to-nitrogen ratio in the soil (Kaye & Hart 1997). In the Southern Tall Grassveld most burning occurs during later winter and in early spring, while thunderstorm activity occurs during early spring through to mid-summer.

The TILLERTREE model assumes that nitrogen can be obtained from the soil at some maximum daily absorption rate per unit root mass (RNuptake). This rate is manipulated using a multiplier variable, mNuptake that represents the environmental availability of soil nitrogen (Equation 3.21, Chapter 3).

For the simulations conducted in the chapters that follow, only the seasonality and discontinuity of soil nitrogen availability were considered as environmental properties affecting the growth of bunchgrass clones. RNuptake was set at 0.001 g N (g wlr)$^{-1}$ d^{-1}. Pulsed activity was ignored. Rather the model assumed that soil nitrogen availability is at maximum during the spring period up until the end of November. Soil nitrogen availability declines linearly through November to zero, where it remains for the remainder of the growing season (Figure 4.1).

Table 4.3   Resource parameter estimates of the model as defined for *Themeda triandra* (sources of estimates are cited)

| Parameter	Blade	Sheath	Internode	Organ — Flower	Root	Other	Source
Transport cost						1.053	Penning de Vries *et al.* 198!
Photosynthesis							
Pmax$_i$						46.364	Coughenour *et al.* 1984
oangle$_{i,j,k}$	**0.67**	0.67	0.67				Assumed
K	0.36 (0.57)	0.36 (0.57)	0.36 (0.57)				Humphreys 1991; Leriche *et al.* 2001
Nitrogen absorption							
RNuptake					0.001		Assumed
Maintenance							
Cmfrlo$_i$	0.0068	0.0068	0.0068	0.0068	0.0102		Penning de Vries *et al.* 198
Growth							
aCgo$_i$	1.326	1.326	1.326	1.426	1.326		Penning de Vries *et al.* 198
aNgo$_i$	0.0302	0.0302	0.0121	0.0121	0.0121		Penning de Vries *et al.* 198
Senescence							
RCdieback$_{i,o}$	0.1	0.1	0.05	0.05	0.05		Assumed
RNdieback$_{i,o}$	0.585	0.585	0.585	0	0.585		Aerts 1996
AVC							
maxAVC						0.1	Assumed
C-Storage							
maxCstore$_{i,o}$	0.1	0.1	0.1	0.1	0.1		Danckwerts 1984; Farrar & Williams 1991
minCstore$_{i,o}$	0.01	0.01	0.01	0.01	0.01		Assumed
RCstore$_i$	0.1	0.1	0.1	0.1	0.1		Farrar & Williams 1991
N-storage							
maxNstore$_{i,o}$	0.01	0.01	0.01	0.01	0.01		
minNstore$_{i,o}$	0	0	0	0	0		Assumed
RNstore$_{i,o}$	0.01	0.01	0.01	0.01	0.01	0.01	Heckathorn & deLucia 19!
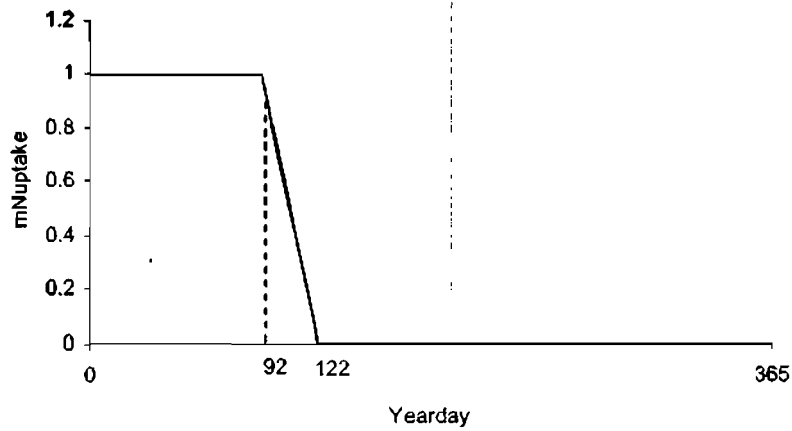
Figure 4.1   Multiplier for daily availability of soil nitrogen (mNuptake) as used for simulations in this thesis. Actual daily nitrogen absorption per unit root mass (RNuptake) is 0.001 g N (g wlr)$^{-1}$ d^{-1} unless specified otherwise. Yearday 1 coincides with 1 September each year, which marks the start of spring in the southern hemisphere.

4   GROWTH LIMITATION BY TEMPERATURE AND SOIL WATER

Air temperature (T) and soil water potential (Ψ_s) are both treated as environmental growth retarders. That is, their effects limit the chemical reaction rates in plants. This affects rates of growth, senescence, maintenance and photosynthesis. In addition their effects are treated as independent, so that growth is retarded by the more limiting of the two environmental parameters on any given day.

4.1   Temperature

The relationships between average daily air temperature (T_{ave}) and plant activity are assumed equal across all activities (maintenance, growth, photosynthesis, senescence), and follow the general bell-shaped curve for enzyme activity in C_4 species (Jones 1985; Ludlow and Wilson 1971; Goudriaan and van Laar 1994). A broken-stick model is used to approximate this relationship.

$$f(T_{ave}) = \begin{cases} 0 & if \quad T_{ave} \leq 5^o C, \\ \dfrac{1}{20} T_{ave} - \dfrac{1}{4} & if \quad 5^o C < T_{ave} \leq 25^o C, \\ 1 & if \quad 25^o C < T_{ave} \leq 35^o C \\ -\dfrac{1}{20} T_{ave} + \dfrac{11}{4} & if \quad 35^o C < T_{ave} \leq 55^o C, \\ 0 & if \quad T_{ave} > 55^o C. \end{cases} \qquad 4.1$$

4.2   Soil water potential

Water stress affects growth more acutely than photosynthesis. The plant process most susceptible to water stress appears to be cell growth, defined as the irreversible expansion of cells (Hsiao & Acevedo 1974). Total and maintenance respiration in grain sorghum both decline when the plant is subjected to slowly developing water stress, although the decline in maintenance respiration was small (Wilson et al. 1980; McCree 1986).

For the simulations, it is assumed that senescence and maintenance are unaffected by soil water pressure. The effects of soil water pressure on growth ($f_g(\Psi_s)$) and photosynthesis ($f_g(\Psi_s)$) are as follows.

$$f_g(\Psi_s) = \begin{cases} 1 & \text{if } \Psi_s > -0.3\ MPa\ , \\ 9\Psi_s + 3.7 & \text{if } -0.4\ MPa < \Psi_s \leq -0.3\ MPa\ , \\ \Psi_s + 0.5 & \text{if } -1.5\ MPa < \Psi_s \leq -0.4\ MPa\ , \\ 0 & \text{if } \Psi_s \leq -1.5\ MPa\ . \end{cases}$$ 4.2

$$f_p(\Psi_s) = \begin{cases} 1 & \text{if } \Psi_s > -0.7\ MPa\ , \\ \dfrac{5}{4}\Psi_s + \dfrac{15}{8} & \text{if } -1.5\ MPa < \Psi_s \leq -0.7\ MPa\ , \\ 0 & \text{if } \Psi_s \leq -1.5\ MPa\ . \end{cases}$$ 4.3

4.3 Simulation of growing and non-growing seasons in annual cycles

The Southern Tall Grassveld is a humid grassland type that has a defined growing season and non-growing season. The non-growing season is induced by low temperature and low soil water pressure. The timing of the non-growing season in the Southern Tall Grassveld varies from year to year in response to climatic variation, but is restricted to fall during the winter months between May and October (Tainton & Booysen 1965).

In the Introduction (Chapter 1) it was emphasised that the aim of this thesis is to explore the effects of interactions between the architecture of bunchgrasses and disproportionate resource allocation to structures in that architecture, on the growth of bunchgrasses. Therefore I ignore daily environmental variability for the actual questions addressed in each of the subsequent chapters, and concentrate on including the major characteristics of the environment. Daily variability in air temperature and soil water potential are only used for the simulations in the next chapter that test the goodness-of-fit of

the model at simulating the growth of individual *Themeda triandra* tillers relative to an independent data set. In all other simulations it is assumed that plant activity is uninhibited by temperature and soil water potential during the growing season and therefore proceeds at the maximum rate, and is inhibited during the non-growing season (Figure 4.2). During the non-growing season growth and photosynthesis are inhibited compltetly and maintenance is reduced to 10% of its growing season value on the assumption that maintenance is required to keep the plant alive. Senescence and decay proceed at maximum rates throughout the year. The enforced non-growing season runs from 1 May to 31 August of each year, which is from Yearday 243 to Yearday 365.

5   INITIATION OF CLONAL GROWTH IN SIMULATIONS

The TILLERTREE model begins a simulation of a clone by initiating the growth of a single ramet with a single tiller. If a tiller is recruited it automatically initiates the growth of its first phytomer. Growth is initiated by providing the first ramet with some internal resources, termed StartAVC and StartAVN. The amounts used are specified in the simulations that follow.

The model also requires an external input file that provides information on the daily environmental data (average temperature; minimum temperature; and soil water potential), and information on defoliation events.
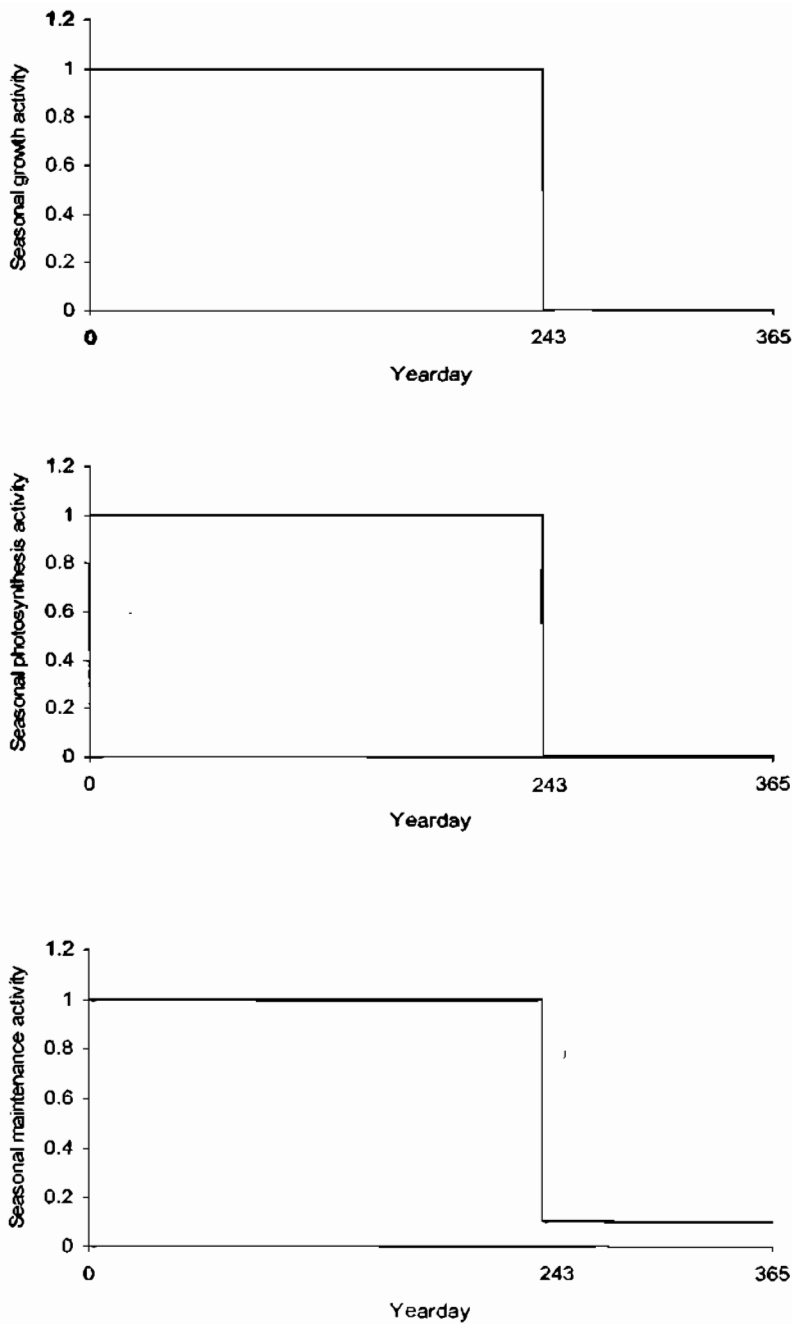
Figure 4.2 Multipliers used to simulate a year cycle that divided is into a growing season and non-growing season. Plant activity is set at maximum value during the growing season, while during the non-growing season growth and photosynthesis are inhibited and maintenance is reduced to 10% of its growing season value. Organ senescence and decay proceed at maximum rates throughout the year.

Chapter 5: Validation of the Structural Behaviour of the Single Ramet Model

In this chapter, it will be verified that structural growth and processing of a single ramet with a single tiller that is prevented from secondary tiller recruitment is both realistic and consistent. This includes looking at its response to defoliation. The model will be verified in a stepwise procedure that will accommodate the different levels of complexity within the model structure in order to build confidence in the model.

Following this, the simulated tiller growth will be compared with an independent empirical data set to demonstrate that it can simulate the growth of *Themeda triandra* reasonably, both in terms of the temporal distribution of growth processes and in terms of the quantitative values simulated. It should be noted that the model can presently only be validated at the single tiller level because there is no empirical data that can be used directly to compare to multiple tiller dynamics generated by the model. Validation at the single tiller level is considered sufficient for this thesis because the analyses in subsequent chapters consider multiple tiller dynamics as determined by interactions between architecture and resource allocation to be the consequence of accumulated individual tiller behaviour.

During this validation process resource limitations are ignored because this complicates the behaviour. In other words, the chapter focuses on validating structural behaviour. However, carbohydrate demand and supply are also presented in order to verify that these function properly in a single-tiller ramet.

1 VERIFICATION OF BEHAVIOUR OF A SINGLE-TILLER RAMET OF *Themeda triandra* UNDER OPTIMAL GROWTH CONDITIONS

A single-tiller ramet contains elements at three levels of construction, namely phytomer-, tiller- and ramet- level. As it is joined to a root system it is an independent, fully functioning plant which grows, reproduces sexually and dies. Since it lacks the ability to reproduce vegetatively through secondary tiller production, it provides a suitable means for analysing the growth and death of an individual tiller grass plant. At this level one can keep sufficient

track of the variables involved in the system in order to interpret the behaviour and demonstrate that it is consistent and realistic with respect to certain critical components.

The environments that bunchgrasses inhabit usually comprise two distinct seasons, a growing season, when the plant expands its biomass if resources are available to do so, and a non-growing season when prevailing environmental conditions prevent growth. Therefore, a first step in assessing the behaviour of the single ramet model is to simplify the system by fixing the abiotic environmental conditions at optimal values during the growing season and sub-optimal values during the non-growing season. This removes unnecessary environmental variability, so that the internally-generated growth behaviour of the clone can be assessed directly. During the growing season, all temperature and water pressure multipliers are set to 1 to allow processes to function at the maximum rate. During the non-growing season, the growth and photosynthesis multipliers are set to 0 to prevent growth and photosynthesis. Maintenance respiration and dieback are allowed to continue during winter as these processes are also obligatory, although respiration is itself much reduced. Dieback is allowed to proceed to ensure that the grass plant begins spring regrowth with minimal live photosynthetic surface.

In these simulation runs, both nitrogen and carbohydrate are non-limiting so that the structural functioning of the model may be demonstrated. The initial resource levels to start the model running are 1.0 g CHO in StartAVC and 0.03 g N in StartAVN. All simulations begin at the start of spring on the 1 September. Ten canopy layers are used so that the functioning of the LAI can be demonstrated easily. Each canopy layer is 100 mm in depth, until the tenth layer which includes all clonal leaf material above 900 mm.

1.1 Phytomer variables

The main variables of individual organs are length and mass, each of which have three components, namely live, dead and total. In addition each organ is able to store carbohydrate and nitrogen. Growth, death and decay of individual organs are correctly represented by the model (Figures 5.1 & 5.2). Importantly the rate of phytomer recruitment slows as the total length of individual phytomer blades increases due to co-ordination of growth between successive phytomers (Skinner & Nelson 1994; Chapter 2). This effect was seen on the tillers observed by Wieners & Morris (2000). The number of phytomers with live leaf material at any one time increases to six initially, and then gradually declines
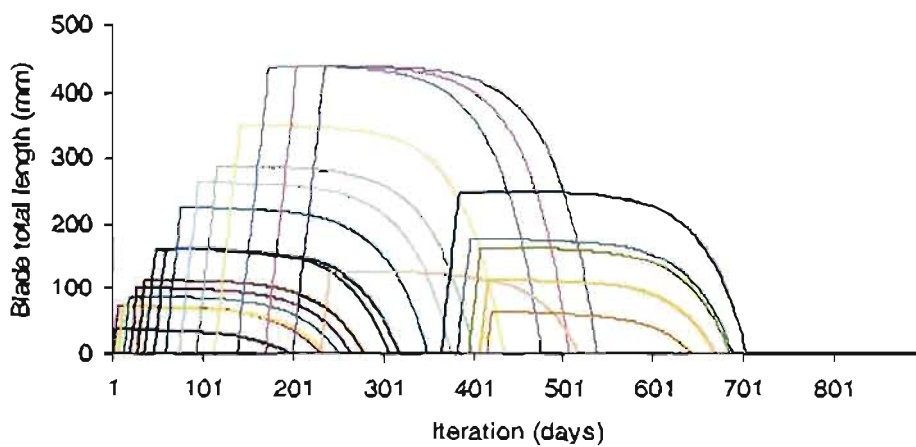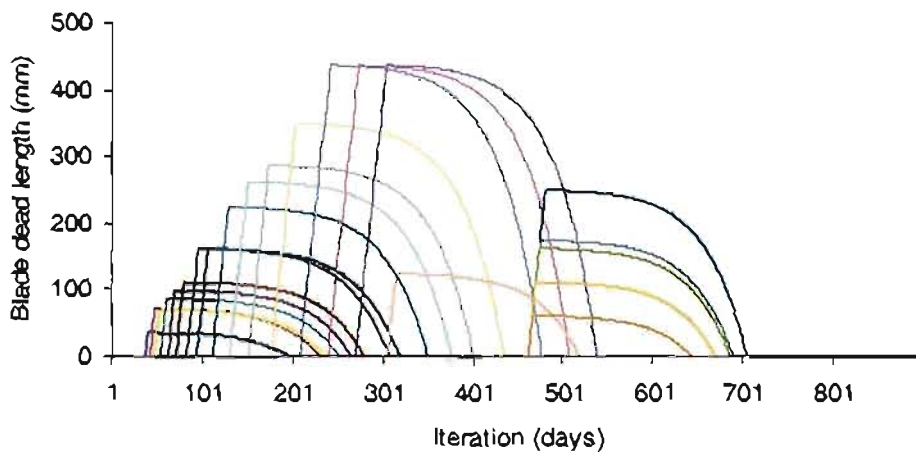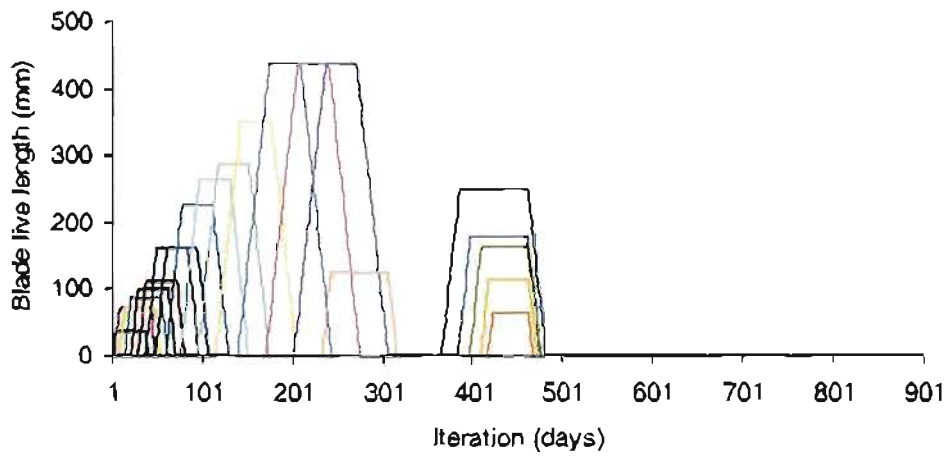
Figure 5.1 Growth, death and decay of blade lengths on consecutive phytomers of a single tiller. (Environmental conditions: Plant activity during the growing and non-growing season as defined in Section 4.3 of Chapter 4. Growing season proceeds from Yearday 1 to Yearday 242 of each year. Soil nitrogen is not limiting to growth.)

through the vegetative period in response to the increased blade lengths of subsequent phytomers. Eventually by the end of the first year there are three to four live leaves at any one time, while the average across the vegetative period is four live leaves. This compares favourably to data collected by Danckwerts (1984) and Wieners & Morris (2000), both of whom recorded average live leaf estimates of 4 leaves during the vegetative phase. Live leaf during the second season increased to 6 in the model, because senescence of blades on culm phytomers only begins after flowers begin to die. The TILLERTREE model recruits a total of 22 phytomers for the modelled *Themeda triandra*. Empirical records of total phytomer number for the *T. triandra* growing under non-restrictive conditions ranges from 23 phytomers (Danckwerts, Aucamp & DuToit 1984) to 24 (Tainton 1967), indicating that the model predicts the turnover of phytomers quite accurately for the species.

Phytomer recruitment halts during winter while live material on blades and sheaths continues to die back during this period. Internode material does not die as it remains alive to support the apical meristem and spring regrowth. It also stores resources during the non-growing season. In spring the blades and sheaths on recruited phytomers begin to grow, but internode expansion is inhibited until after the second flowering phase phytomer has been recruited (Figure 5.2). In addition internode expansion is subsequent to the completion of blade expansion, which staggers the extension of phytomers on *T. triandra* culms. There are two inflorescences each placed on the fifth and sixth flower phase phytomers, but they are cued to only start growing once the sixth phytomer has been initiated. Since they have identical growth potentials, their values are identical in the present simulation (Figure 5.2). Internodes on phytomers recruited before winter increase their mass exponentially because of the iterative stem mass deposit described in the model (Chapter 2). This also occurs on post-winter phytomers as can be seen from the broken stick function of internode mass growth, where the first piece represents internode elongation and mass gain and the second piece represents mass gain alone.

Decay of organs extends the simulation run quite substantially because it is consecutive to death and because decay follows an exponential form. Once all organ material has decayed back to zero, the tiller is destroyed and the simulation ends.

In order to demonstrate that resource storage is functioning correctly in the model, carbohydrate storage ($Cstore_{o,t}$) was fixed to 0.1 times the live mass of individual organs and nitrogen storage ($Cstore_{o,t}$) was fixed to 0.01 times the live mass of individual organs. Carbohydrate and nitrogen storage in internodes is shown (Figure 5.3). In the present
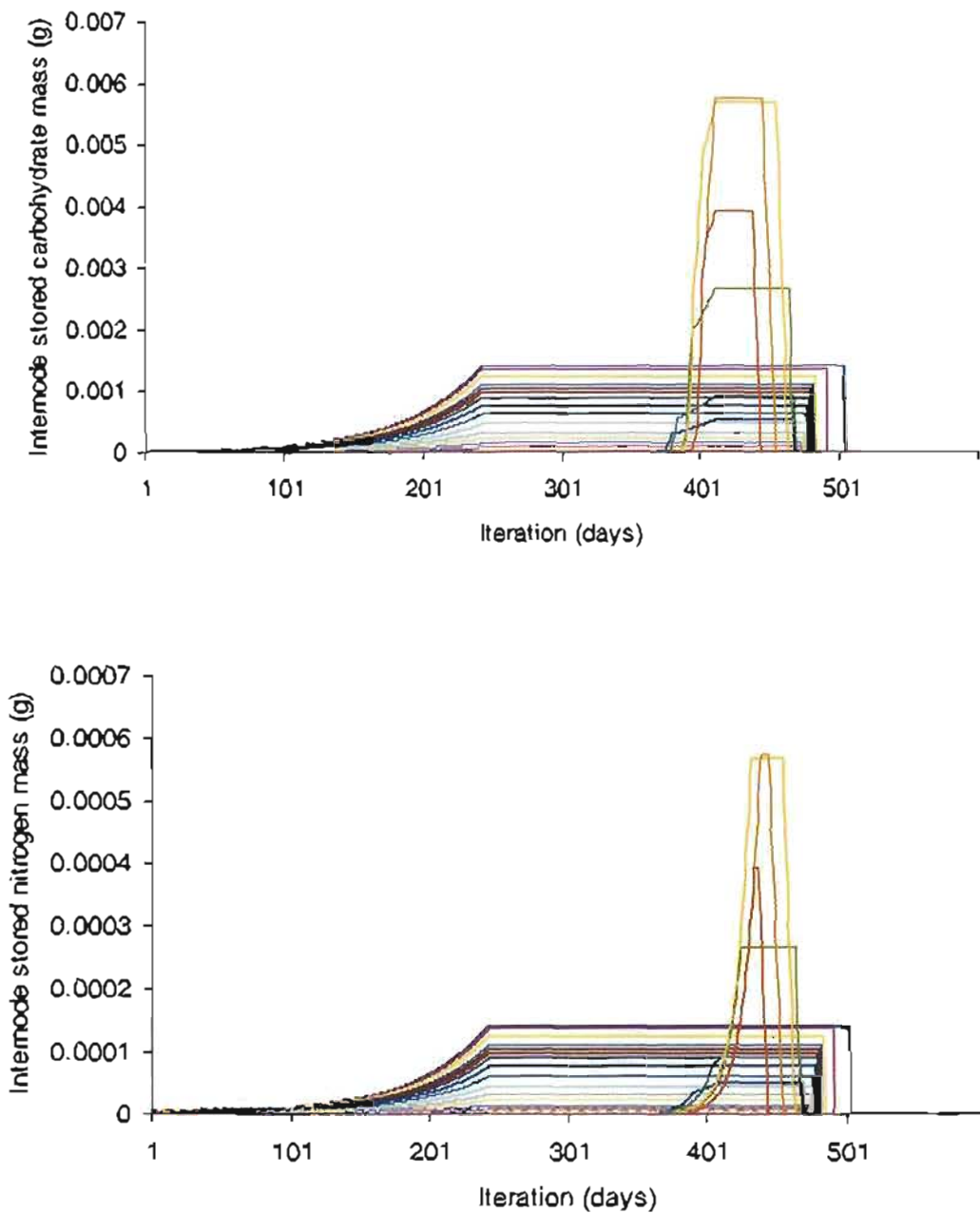
Figure 5.3 Nutrient storage in internodes on consecutive phytomers of a single tiller, where carbohydrate storage is fixed at 0.1 of organ live mass and nitrogen storage is fixed at 0.01 of organ live mass. (Environmental conditions: Plant activity during the growing and non-growing season as defined in Section 4.3 of Chapter 4. Growing season proceeds from Yearday 1 to Yearday 242 of each year. Soil nitrogen is not limiting to growth.)

simulation the tiller does not experience stress that limits its resources, so storage is optimal at all times during the simulation.

The proper function for seasonal carbohydrate storage, as outlined in Chapter 3, is introduced at this stage and its effect on organ storage in shown in Figure 5.4. Carbohydrate storage decreases sharply in spring in response to low photosynthetic rates. Storage values continue to rise and fall in response to the ratio of supply to demand during the sexual reproduction period. Towards the end of sexual reproduction the growth demand decreases which allows more resources to be allocated to storage.

1.2 Tiller variables

Summed organ masses proceed through a series of phases that relate to phenophase and to the non-growing period over winter (Figure 5.5). The vegetative phase (Phenophase 1) is in the first season and is characterised by leaf production and no stem elongation. Stem elongation and flowering are cued in the second spring when the tiller enters the sexual reproductive phase (Phenophase 2) and two of the flowering phase phytomers have been initiated. There is also substantially less leaf production during this period. Once flowering is complete, the tiller enters Stasis (Phenophase 3) and begins programmed death of all live structures. The tiller dies (Phenophase 4) when all component organs on the tiller have died back sufficiently to satisfy the mortality rules (Chapter 3).

Initially stem dieback was set at 12.5 mm d^{-1}, but this meant that the tiller took over 100 days to dieback to the base and complete senescence after flowering, which was too long when compared to the dieback of culms of *Themeda triandra* growing under field conditions (personal observation). Therefore stem dieback was doubled to 25 mm d^{-1} to increase the rate of dieback. Part of the problem here probably relates to the fact that stem dieback in the model is sequential backwards in order to prevent the loss of live organs. In reality dieback occurs as co-ordinated cell deconstruction along the entire organ on a particular phytomer if that phytomer is not acting as a conduit to link active meristems. Increasing the internode dieback rate increased the senescence rate of the tiller subsequent to reproduction.
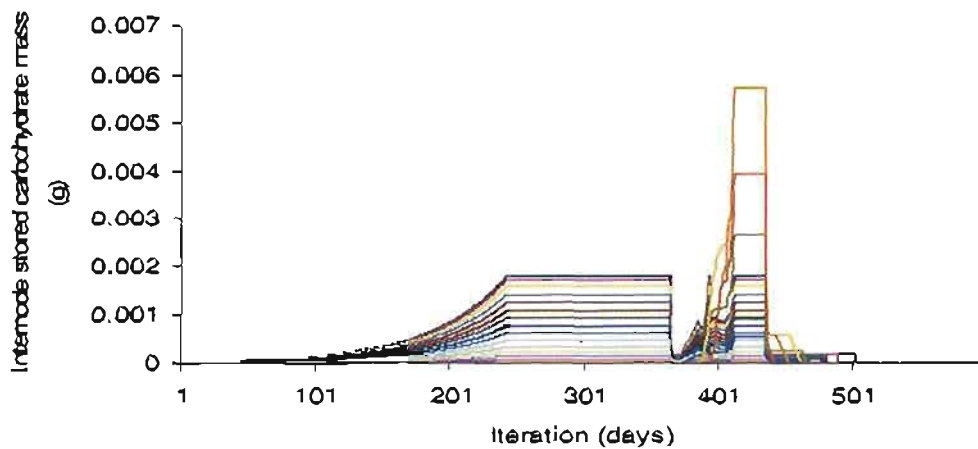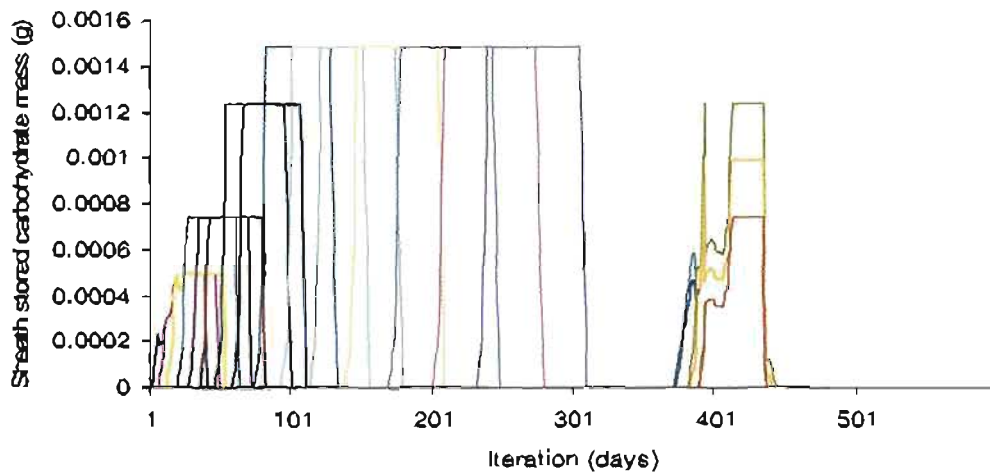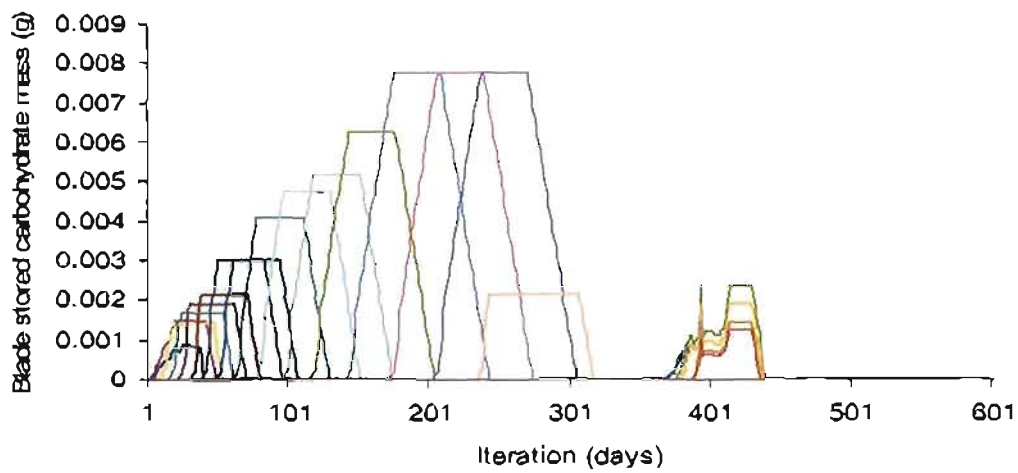
Figure 5.4 Seasonal shifts in carbohydrate storage in organs on consecutive phytomers of a single tiller. (Environmental conditions: Plant activity during the growing and non-growing season as defined in Section 4.3 of Chapter 4. Growing season proceeds from Yearday 1 to Yearday 242 of each year. Soil nitrogen is not limiting to growth.)

Figure 5.5 Summed live mass of organ types on an individual tiller (— · — blade mass; ———— sheath mass; — ·· — internode mass; — — — flower mass). (Environmental conditions: Plant activity during the growing and non-growing season as defined in Section 4.3 of Chapter 4. Growing season proceeds from Yearday 1 to Yearday 242 of each year. Soil nitrogen is not limiting to growth.)
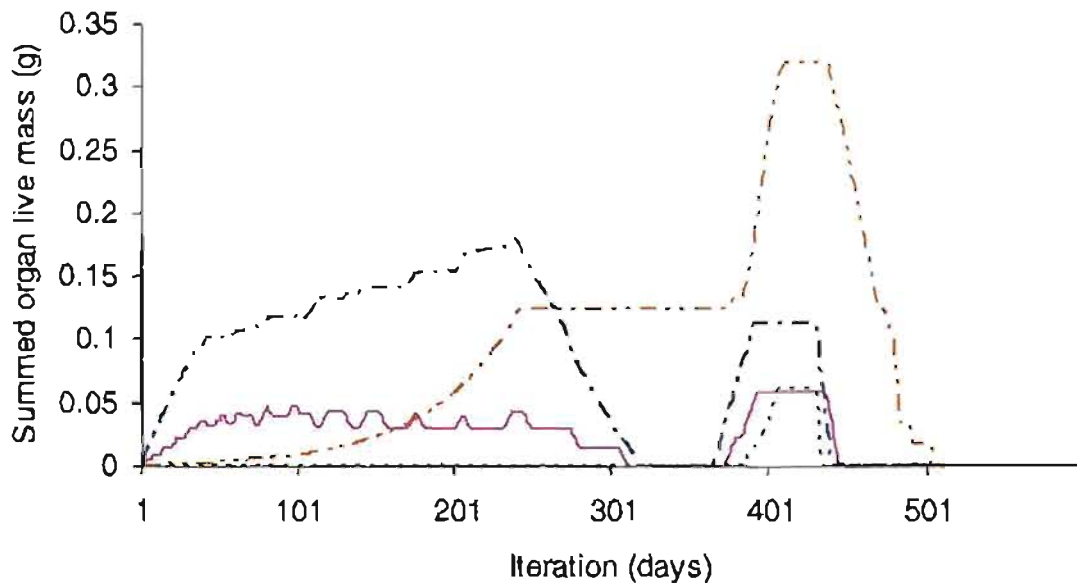

Figure 5.6 Daily carbohydrate demand and supply of a single-tiller ramet that has no nitrogen or carbohydrate limitation. (Dark blue = net photosynthesis supply; pink = maintenance demand; orange = growth demand; pale blue = storage demand; purple = dieback supply.) (Environmental conditions: Plant activity during the growing and non-growing season as defined in Section 4.3 of Chapter 4. Growing season proceeds from Yearday 1 to Yearday 242 of each year. Soil nitrogen is not limiting to growth.)
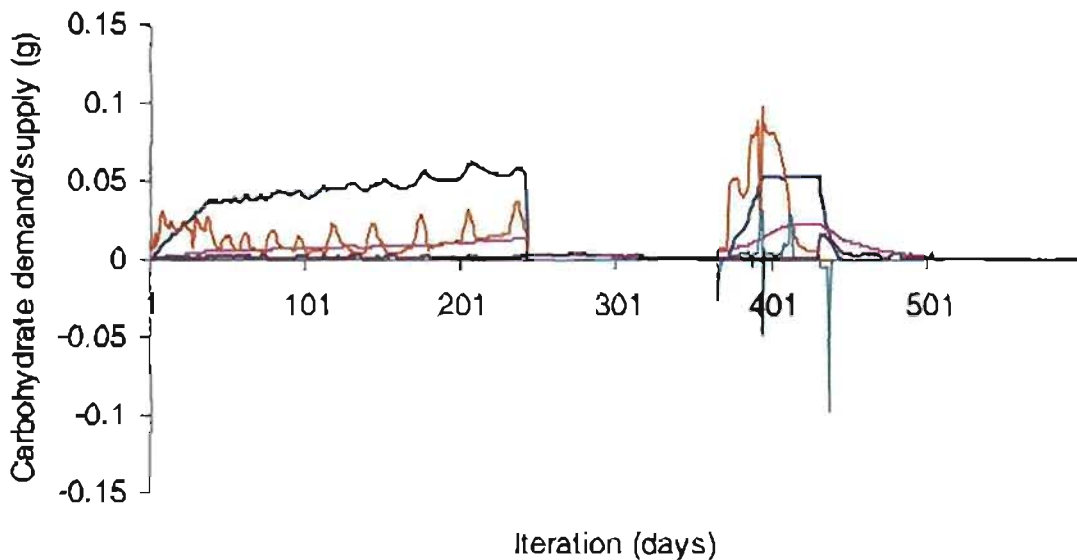
Figure 5.7   Change in root mass (————) and shoot mass (— — —) of a single-tiller ramet that has no nitrogen or carbohydrate limitation. (Environmental conditions: Plant activity during the growing and non-growing season as defined in Section 4.3 of Chapter 4. Growing season proceeds from Yearday 1 to Yearday 242 of each year. Soil nitrogen is not limiting to growth.)
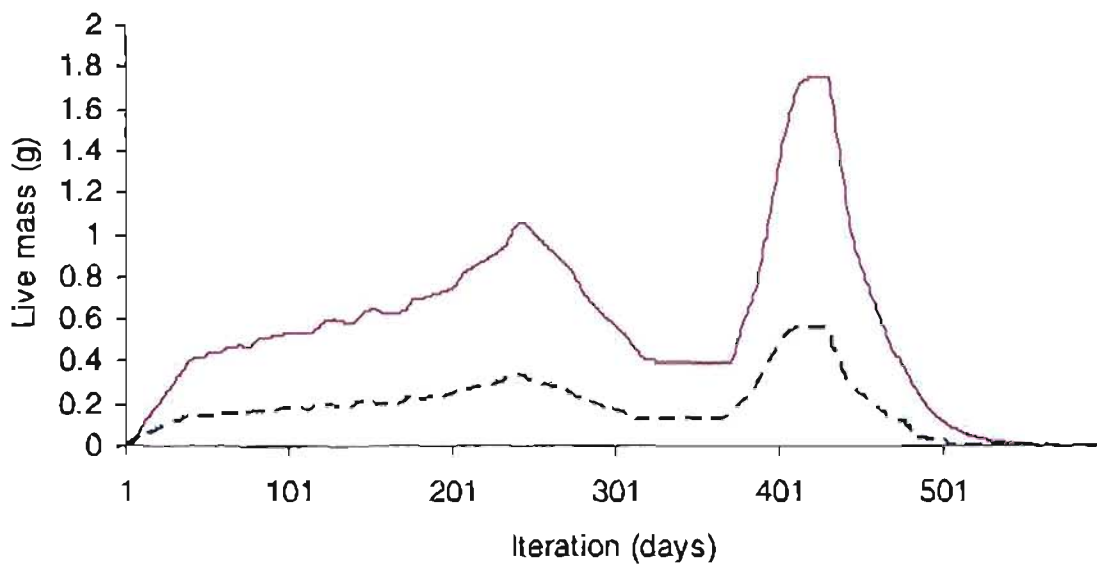

Figure 5.8   Daily mass of available non-structural carbohydrate (AVC) of a single-tiller ramet. Because storage is not limited in this simulation, AVC represents the accumulated CHO excess of the system. (Environmental conditions: Plant activity during the growing and non-growing season as defined in Section 4.3 of Chapter 4. Growing season proceeds from Yearday 1 to Yearday 242 of each year. Soil nitrogen is not limiting to growth.)
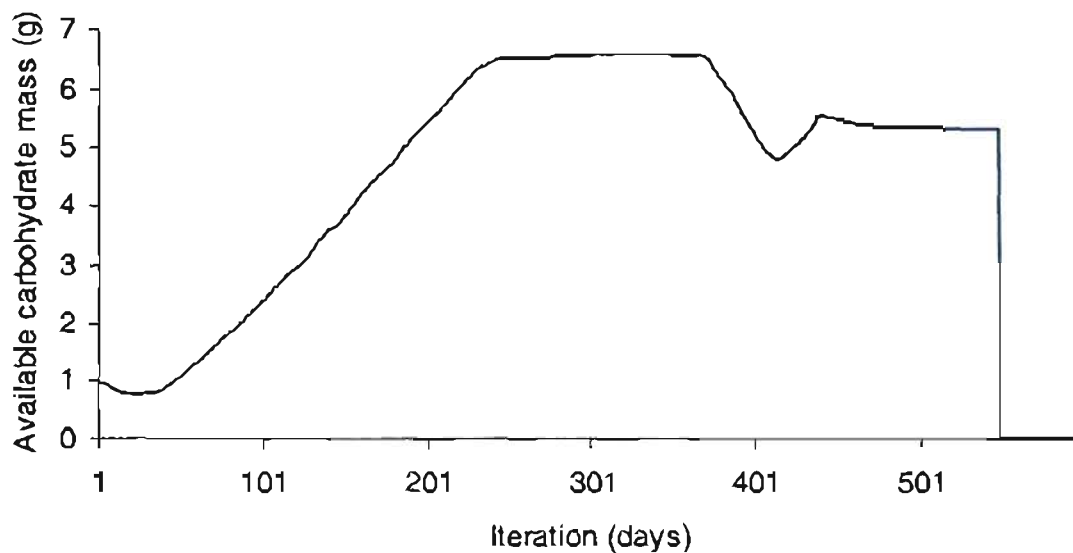
the plant over the life of the plant. The seasonal accumulation of carbohydrate production and carbohydrate demand generated by the model indicates that although total photosynthate production exceeds total demands, photosynthate production in the second season is less than carbohydrate demand during that season (indicated by the dip in accumulated carbohydrate in Figure 5.8). This means that model growth in the second spring relies on a substantial amount of carbohydrate generated in the first season, which is unrealistic given the small amount of storage in over-wintering tillers. This indicates that the present fixed ideal root-to-shoot ratio, $awllb_{i,t}$, of 3.2 cannot be supported by the single-tiller ramet. The next chapter concentrates on resource allocation when storage is limited.

Photosynthetic production during the second spring is restricted by the limited photosynthetic surface constructed during the second season and the reduction of photosynthetic production due to light inhibition by the surrounding canopy (Figure 5.9). Presently leaf area index (LAI) is set equal to the sum of BAI and SAI only. This is because internodes of *Themeda triandra* are brown and as such are assumed to be non-photosynthetic. Therefore they remove an insignificant amount of the photosynthetically active radiation. The peak leaf area index is achieved by a tiller during its vegetative growth phase due to the large surface area of leaf blades.

The effect of LAI above each layer on the photosynthetic rate within that layer, $F_p(LAI)$, shows the clear inverse relationship with LAI (Figure 5.10). The net effect on photosynthetic efficiency of photosynthetic tissues is indicated (Figure 5.11) showing that photosynthesis is strongly impacted during the second spring, both during regrowth after winter and during senescence after flowering. The restriction in early spring arises because all blades and sheathes die back over winter so new phytomers have to expand from the apical bud in the second spring. The apical meristem remains close to the ground through the early part of the second growing season so new blades and sheaths start growing below most of the aerial plant matter and experience strong light restriction.

1.4 Growth response to defoliation

The model treats grazing and burning as distinct types of defoliation. Herbivore grazing is imposed as a height cut above which all plant material, live and dead, is removed. Burning removes all live and dead material above the specified burn height and kills all live sheath
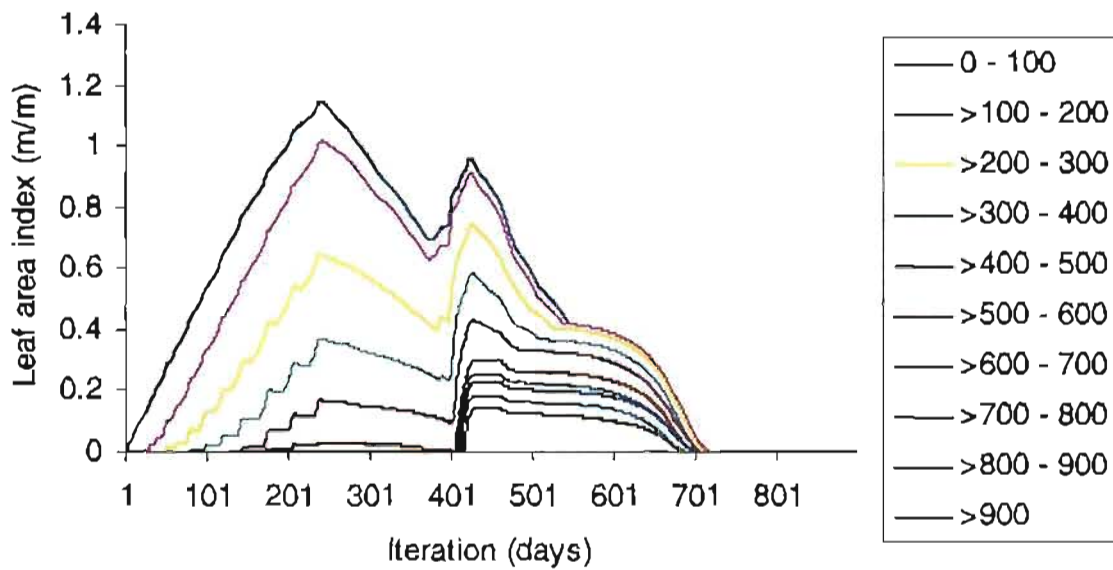
Figure 5.9 Leaf area index (LAI) in different height layers as they change over time for a single-tiller ramet. (Environmental conditions: Plant activity during the growing and non-growing season as defined in Section 4.3 of Chapter 4. Growing season proceeds from Yearday 1 to Yearday 242 of each year. Soil nitrogen is not limiting to growth.)
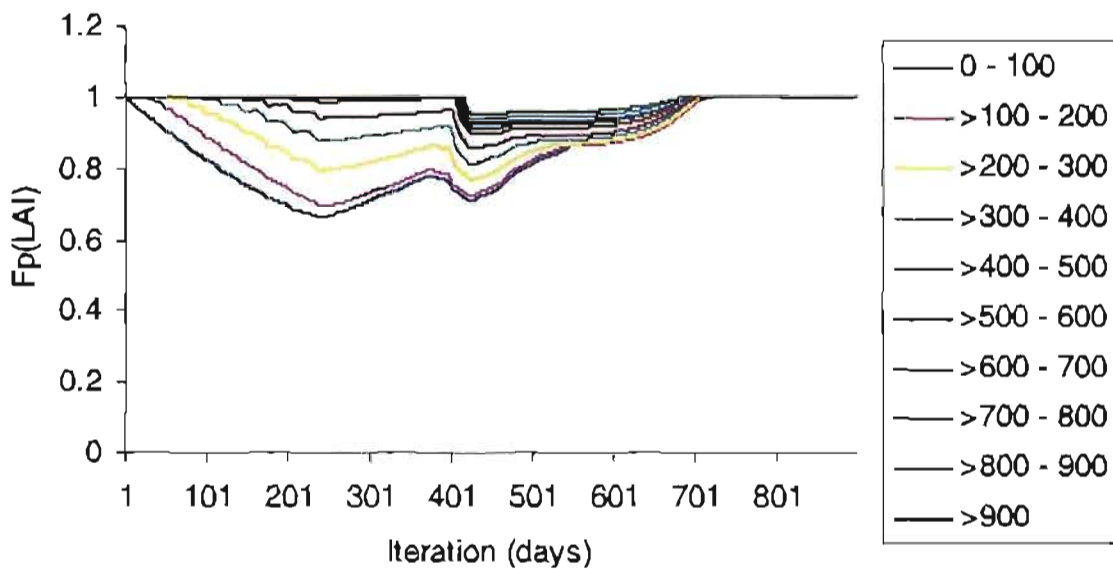
Figure 5.10 Photosynthetic leaf area index multiplier (F_p(LAI)) in each height layer on a single-tiller ramet. The F_p(LAI) represents the level to which light is dissipated by intervening plant material in the shoot canopy, and therefore is inversely proportional to the LAI at any given height in the canopy. (Environmental conditions: Plant activity during the growing and non-growing season as defined in Section 4.3 of Chapter 4. Growing season proceeds from Yearday 1 to Yearday 242 of each year. Soil nitrogen is not limiting to growth.)

Figure 5.11 Efficiency of photosynthetic tissues (blades and sheaths) on a single-tiller ramet. (Environmental conditions: Plant activity during the growing and non-growing season as defined in Section 4.3 of Chapter 4. Growing season proceeds from Yearday 1 to Yearday 242 of each year. Soil nitrogen is not limiting to growth.)
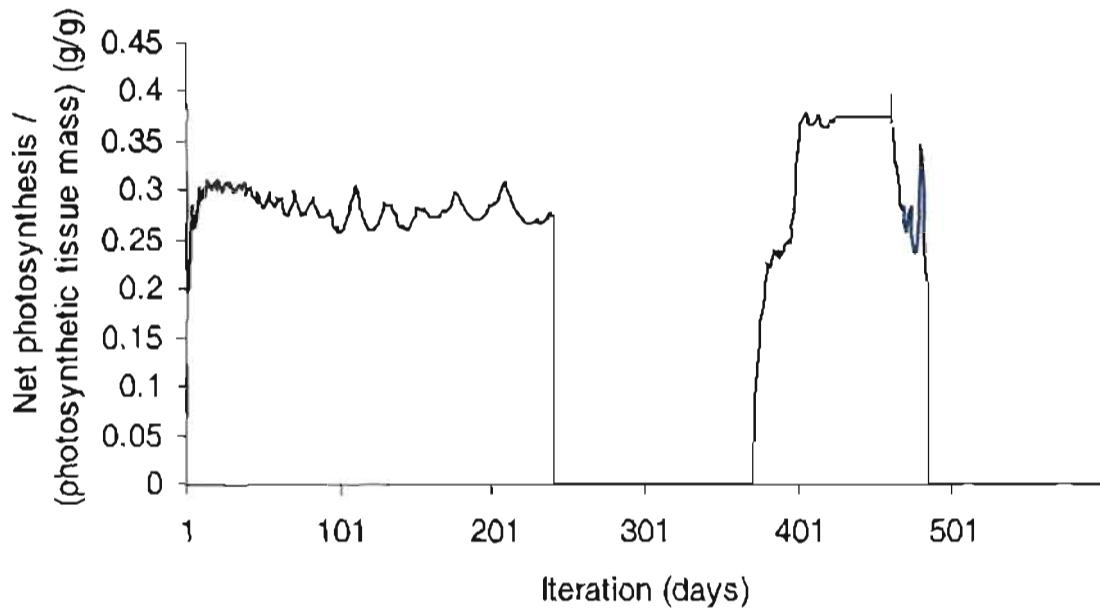
and blade material below the burn height. Live stem material below the burn height is not destroyed. Cutting is used to demonstrate the response of the model to defoliation.

For the simulation two cuts were applied annually on day 86 and day 184 at a height of 60 mm for both events. Total masses of individual organs (Figure 5.12), summed live masses of organ types (Figure 5.13) and shoot mass (Figure 5.14) were reduced abruptly by each defoliation event. The imbalance in the actual root-to-shoot ratio induces root dieback, which releases additional carbohydrate for allocation to shoot growth. The defoliation event also removes overlying dead material, which allows more light to penetrate to the new phytomers. This increases the photosynthetic efficiency of the remaining leaf surface after each defoliation event. The first defoliation event in the second year of growth (iteration 451) removed all live blade and sheath material and removed the stem to a height of 60 mm above the ground as specified for this simulation. This decapitated the apical meristem and forced the tiller into Stasis (Phenophase 3). Death followed rapidly and the simulation was completed more quickly (less iterations) because the amount of material available to decay was much reduced by the defoliation events.

2 COMPARISON OF SIMULATED DATA WITH EMPIRICAL DATA UNDER NATURAL ENVIRONMENTAL CONDITIONS

In order to demonstrate that the model predicts the growth of *Themeda triandra* tillers with sufficient accuracy, it is necessary to compare the behaviour of tillers generated by the TILLERTREE model to *T. triandra* tillers growing under natural conditions. The data of an ontogenetic study of individual tiller growth *of T. triandra* in response to different defoliation treatments by Tainton & Booysen (1965) is suitable for such an analysis. This study was conducted at Ukulinga, so the same *T. triandra* ecotype has been used to parameterise the model (Chapter 4) as was measured by Tainton & Booysen (1965), making the data directly comparable.

At this point it is necessary to point out that the extension growth of individual organs responds to the incident R:FR ratio of the local environment. Low R:FR stimulates organs to extend to greater potential lengths, while high R:FR stimulates tillers to grow to minimal potential lengths. Therefore individual tiller size is partly determined by the local light environment. In this section the model's performance is tested against the average estimates recorded by Tainton & Booysen (1965) for tillers recruited at the start of spring
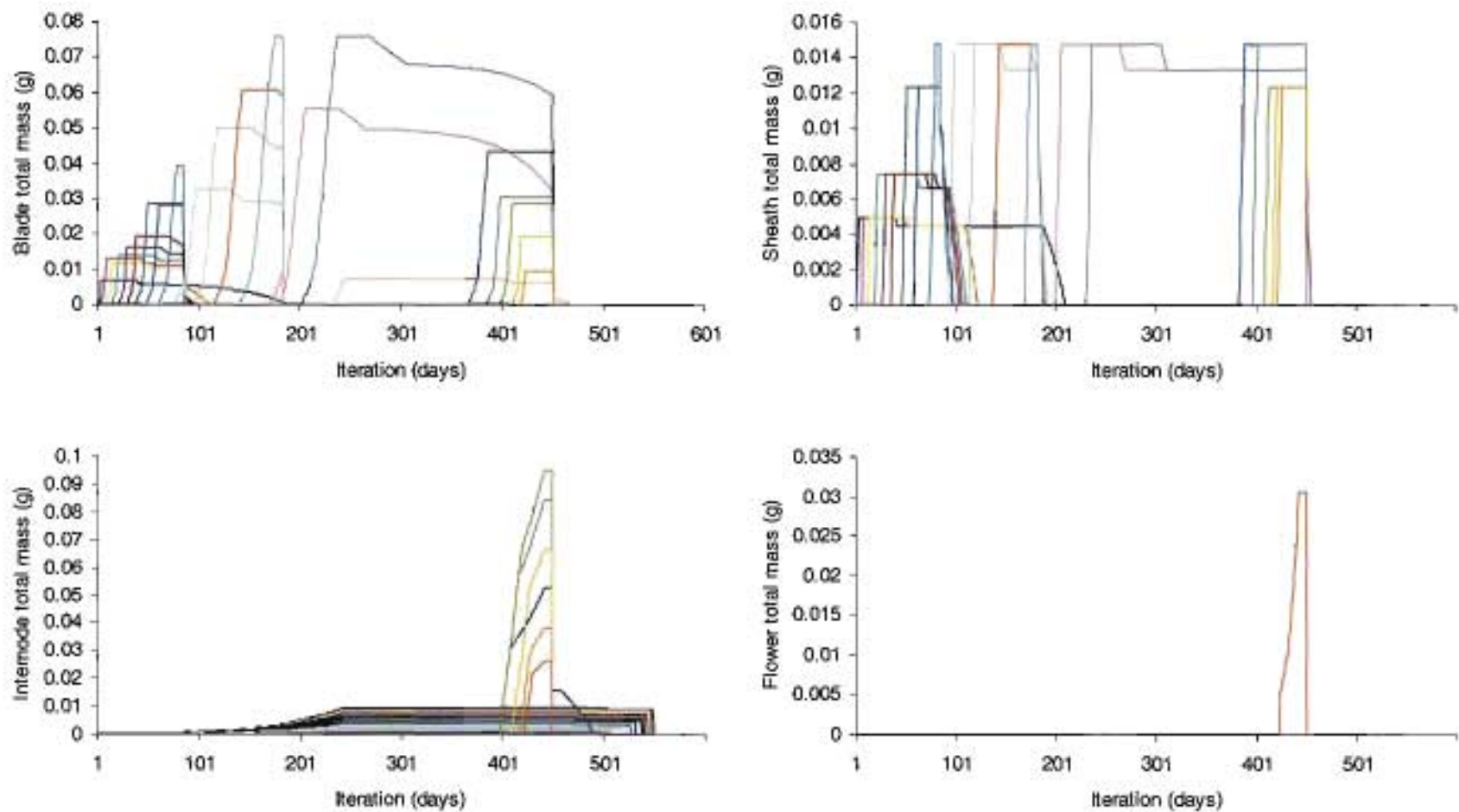
Figure 5.12   Total organ masses on a single-tiller ramet subjected to cutting defoliation. Treatment: cut height = 60 mm, applied annually on day 86 and day 184. The R:S ratio is fixed at 3.2 at all times. (Environmental conditions: Plant activity during the growing and non-growing season as defined in Section 4.3 of Chapter 4. Growing season proceeds from Yearday 1 to Yearday 242 of each year. Soil nitrogen is not limiting to growth.)
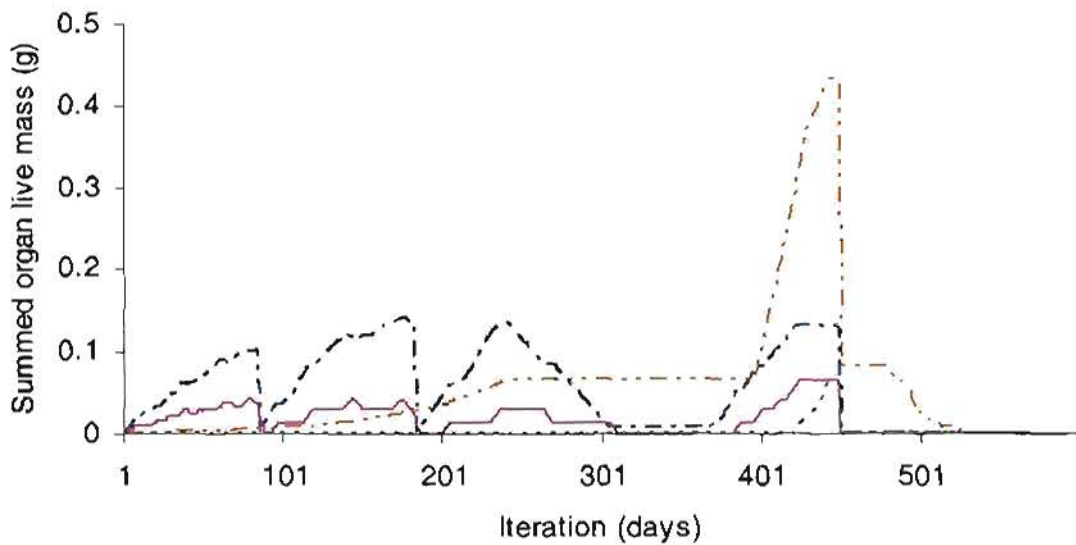
Figure 5.13 Summed live mass of organ (— · — blade mass; ———— sheath mass; — · · — internode mass; — — — flower mass) of a single-tiller ramet subjected to a cutting treatment. Treatment: cut height = 60 mm, applied annually on day 86 and day 184. Carbohydrate storage is restricted while N is not restricted. The R:S ratio is fixed at 3.2 at all times. (Environmental conditions: Plant activity during the growing and non-growing season as defined in Section 4.3 of Chapter 4. Growing season proceeds from Yearday 1 to Yearday 242 of each year. Soil nitrogen is not limiting to growth.)

Figure 5.14 Change in live root mass (————) and live shoot mass (— — —) of a single-tiller ramet subjected to a cutting treatment. Treatment: cut height = 60 mm, applied annually on day 86 and day 184. Carbohydrate storage is restricted while N is not restricted. The R:S ratio is fixed at 3.2 at all times. (Environmental conditions: Plant activity during the growing and non-growing season as defined in Section 4.3 of Chapter 4. Growing season proceeds from Yearday 1 to Yearday 242 of each year. Soil nitrogen is not limiting to growth.)
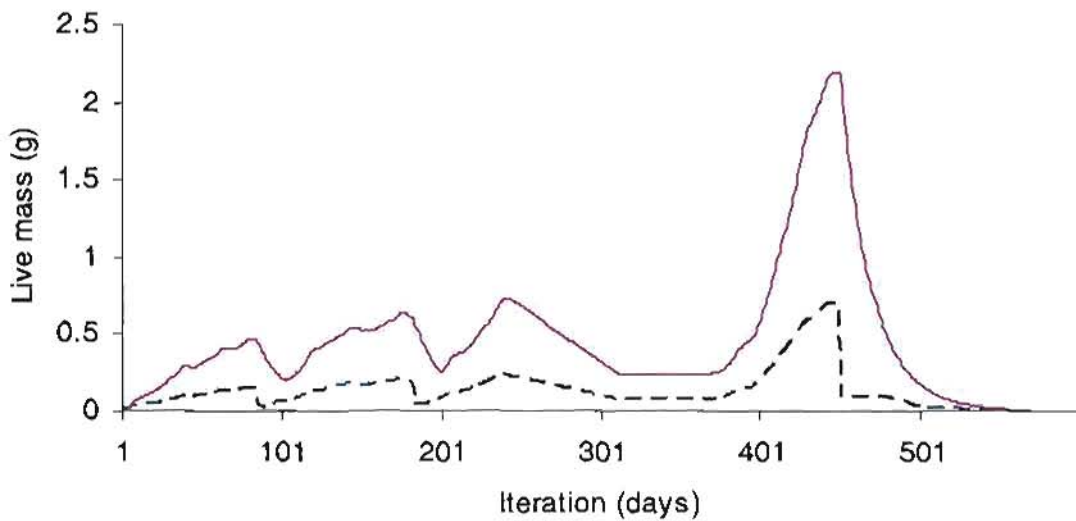
that grew in a sward that was only defoliated just before the tillers were initiated and never again during the development of the tillers. Data collected at Ukulinga for the present study included an identical treatment, called the No Defoliation treatment (Appendix A1). Therefore organ extension data obtained from this treatment, presented in Table 4.1 in Chapter 4 is used for the simulations that follow to improve the comparison of the simulated data and the empirical data of Tainton & Booysen (1965).

In order to compare the simulated data to the empirical data, it is necessary to include the environmental variables that restrict growth. Therefore the functions that restrict growth in response to average air temperature, $f_g(T_{ave})$, and soil water pressure, $f_g(\Psi_s)$ as presented in Chapter 4, are included in the model for this simulation. Data for Ψ_s and T_{ave} is supplied for the years 1961 to 1963, to match the field data collected by Tainton & Booysen (1965). Environmental data (average temperature, minimum temperature, soil water potential) for the Ukulinga site for the years when Tainton & Booysen (1965) conducted their study was obtained using the ACRU Agrohydrological Model (Schulze 1995).

The data set collected by Tainton & Booysen (1965) contains a limited number of parameters. Importantly, all organ mass measurements were taken as tiller total (live plus dead) mass. Also the data set did not divide leaves into sheaths and blades, but rather treated them as one component. Summed leaf parameters are easily calculated from the model. Stem material is live throughout the growing phase of the tiller, so this parameter can be compared directly. Most important in the validation process is comparison of the temporal distribution of growth processes and how closely the model follows the empirical data. It is anticipated that there will be some discrepancy between masses simulated during the reproductive phase and the empirical data because the data set used for the organ parameters was calculated from tillers that were larger than those measured by Tainton & Booysen (1965) (see Appendix A1). Reference will be made to the data set in Appendix A1 when differences arise in order to validate some results predicted by the model that appear to be different to the data collected by Tainton & Booysen (1965).

The decay rate parameter, RDecay, was an unknown parameter. Therefore a number of simulations were conducted with different values for RDecay in order to establish a value that generated similar data to that of Tainton & Booysen (1965). It was concluded that a value of $0.012 \text{ g}^{-1} \text{ g}^{-1} \text{ d}^{-1}$ gave a similar representation to the data presented by Tainton & Booysen (1965) and this was used as a measure for the decay of *Themeda triandra* in the model. The growth of a single tiller ramet was then simulated again for comparison with the

empirical data of Tainton & Booysen (1965). No other parameter or growth pattern was tweaked for this simulation.

The simulated data is compared to the empirical data in two ways. Firstly the simulated data and empirical data are compared non-rigorously, using maximum values for certain seasonal parameters. Secondly the simulated data and empirical data are compared rigorously by graphical comparison of the seasonal growth behaviour visually and by using a formal statistical analysis of goodness-of-fit.

2.1   Seasonal growth maxima

Seasonal growth maxima during the vegetative and reproductive phases of development are presented in Table 5.1. The model predicts that 18 phytomers are recruited during the lifetime of the tiller, which is very similar to the empirical value of 17.4 recorded by Tainton & Booysen (1965). Obviously growth periods coincide between the empirical data and the simulated data because the same environmental data was used to run the simulation. Therefore it seems apparent that the model captures the seasonal distribution of phytomer recruitment reasonably well.

The actual values of, and correlation between, mass and length estimates of the simulated and empirical data is reasonably satisfactory with a few exceptions. Summed total blade length is greater during the reproductive phase than the vegetative phase, which agrees with the empirical data. However the simulated values are smaller than the empirical values in both growth periods. This naturally affected total tiller mass as well.

Simulated stem length and mass at full reproductive length are much greater than the empirical data, but this was anticipated previously. As mentioned briefly, the culm length achieved here for *Themeda triandra* is based on data collected for the species at Ukulinga (recorded Appendices A1 and A2).

Table 5.1   Comparison of tiller growth maxima of *Themeda triandra* generated by the adjusted simulation of the TILLERTREE model and actual empirical data collected by Tainton & Booysen (1965)

Tiller parameter	Model estimate	Empirical estimate
General		
Total phytomers recruited	**18**	17.4
Date max apical elevation attained	18 November	Late November
Vegetative phase (first season)		
Maximum total leaf mass (g)	0.381	0.44
Maximum total internode mass (g)	0.059	0.07
Maximum total tiller mass (g)	0.489	0.51
Maximum stem length (mm)	72.81	80
Total leaf lengths (mm)	2324.33	2700
Reproductive phase (second season)		
Maximum total leaf mass (g)	0.489	0.59
Maximum total internode mass (g)	0.351	0.20
Maximum total inflorescence mass (g)	0.098	0.10
Maximum total tiller mass (g)	0.890	0.89
Maximum stem length (mm)	802.1	520
Total leaf lengths (mm)	2853.29	3300

2.2   Seasonal growth distribution and goodness-of-fit

2.2.1   The Mean Square Error (MSE) and error decomposition

Goodness-of-fit of the simulated data to the empirical data was tested using an elegant decomposition of the mean square error (MSE) (Theil 1961). A description of this method is summarised from Sterman (1984).

The MSE is defined as:

$$\frac{1}{n}\sum_{t=1}^{n}(S_t - A_t)^2 \qquad\qquad 5.1$$

where,   n = number of observations (t = 1,...,n)

S$_t$ = simulated values at time t

A$_t$ = actual value at time t.

The root-mean-square-percentage error (RMSPE) is a normalisation that allows the size of the differences to be interpreted more easily.

$$\sqrt{\frac{1}{n}\sum_{t=1}^{n}\left[\frac{(S_t - A_t)}{A_t}\right]^2} \cdot \qquad\qquad 5.2$$

The MSE can be decomposed into a three components that provide separate information about the nature of the differences between the simulated data and the actual data.

$$\frac{1}{n}\sum_{t=1}^{n}(S_t - A_t)^2 = (\overline{S} - \overline{A})^2 + (S_S - A_S)^2 + 2(1-r)S_S A_S \cdot \qquad 5.3$$

$\overline{S}$ and $\overline{A}$ are the means of S and A respectively, and S$_S$ and A$_S$ are the standard deviations of S and A respectively, i.e.

$$S_S = \sqrt{\frac{1}{n}\sum(S_t - \bar{S})^2} .$$

5.4

$$A_S = \sqrt{\frac{1}{n}\sum(A_t - \bar{A})^2} .$$

5.5

Finally r equals the correlation coefficient between simulated and actual data.

$$r = \frac{\frac{1}{n}\sum(S_t - \bar{S})(A_t - \bar{A})}{S_S A_S} .$$

5.6

The term $(\bar{S} - \bar{A})^2$ measures the bias between simulated and actual data. Bias can be thought of as the translation of one series by a constant amount at all points in time. The term $(S_S - A_S)^2$ measures the degree of unequal variation between the two series. Finally the term $2(1 - r)S_S A_S$ represents the component of error due to incomplete covariance between the two series, which is the degree to which the changes in the simulated series fail to match the actual series on a point-by-point basis.

By dividing each of the components of error by the total mean-square error, the inequality proportions are derived, where U^M, U^S, U^C represent the fraction of MSE due to bias, unequal variance and unequal covariance respectively.

$$U^M = \frac{(\bar{S} - \bar{A})^2}{\frac{1}{n}\sum_{t=1}^{n}(S_t - A_t)^2} .$$

5.7

$$U^S = \frac{(S_S - A_S)^2}{\frac{1}{n}\sum_{t=1}^{n}(S_t - A_t)^2} .$$

5.8

$$U^C = \frac{2(1-r)S_S \, A_S}{\frac{1}{n}\sum_{t=1}^{n}(S_t - A_t)^2}. \qquad\qquad 5.9$$

$$U^M + U^S + U^C = 1. \qquad\qquad 5.10$$

A large bias with small unequal variance and unequal covariance indicates a systematic difference between the model and reality at all times. However systematic errors may also occur due to unequal variance when bias and unequal covariance are small because the mean values and series trends of the actual and simulated data are similar while their distribution of points may be stretched apart. A large covariance indicates that the majority of error is unsystematic with respect to the purpose of the model, and the model should not be faulted for failing to match the random component of the data.

In summary, a good model should have small error (small RMSPE) that is unsystematic (i.e. concentrated in U^C and U^S). Large total errors need not compromise the utility of the model if they are due to excluded modes or noise in the empirical data. Conversely, large biases or unequal trend errors should lead to questions about assumptions of the model.

2.2.2 Model performance

The statistics above were applied to points selected from simulated data that match the empirical data set by date in the season. The compared series are shown graphically in Figures 5.15 to 5.19 and the summary statistics are presented in Table 5.2. The graphics indicate the number of points compared as derived from the empirical estimates.

The data in Table 5.2 indicates that the RMSPE is less than 1% for three of the considered parameters and less than 5% for the two other parameters, and as such we may deduce that the simulated data matches the empirical estimates very well. Stem length is greater than 4%, but the parameter shows large unequal covariance (U^S) relative to the other error fractions. When one considers the shape of the two stem parameter graphs, it is possible that with greater sampling density the RMSPE values of both stem parameters might increase slightly. The larger RMSPE of stem length is of course due to the much

74

Figure 5.15   Comparison of summed leaf total length of simulated values and empirical estimates for the years 1961-62 at Ukulinga (—— simulated; ♦ empirical). (Environmental conditions: Plant activity restricted by daily temperature and soil water pressure data for the site, as defined in Sections 4.1 and 4.2 of Chapter 4. Soil nitrogen is not limiting to growth.)
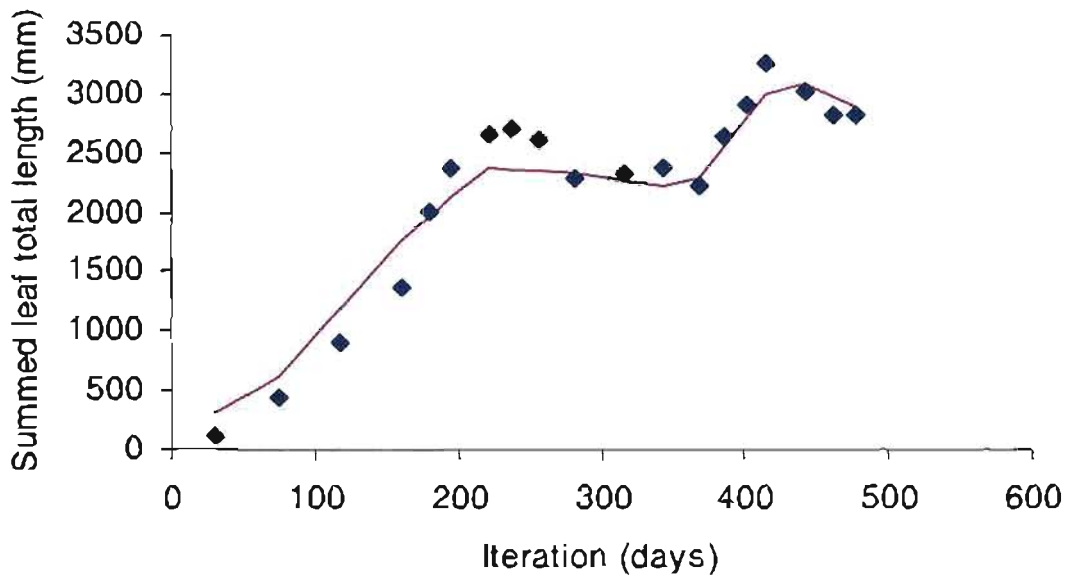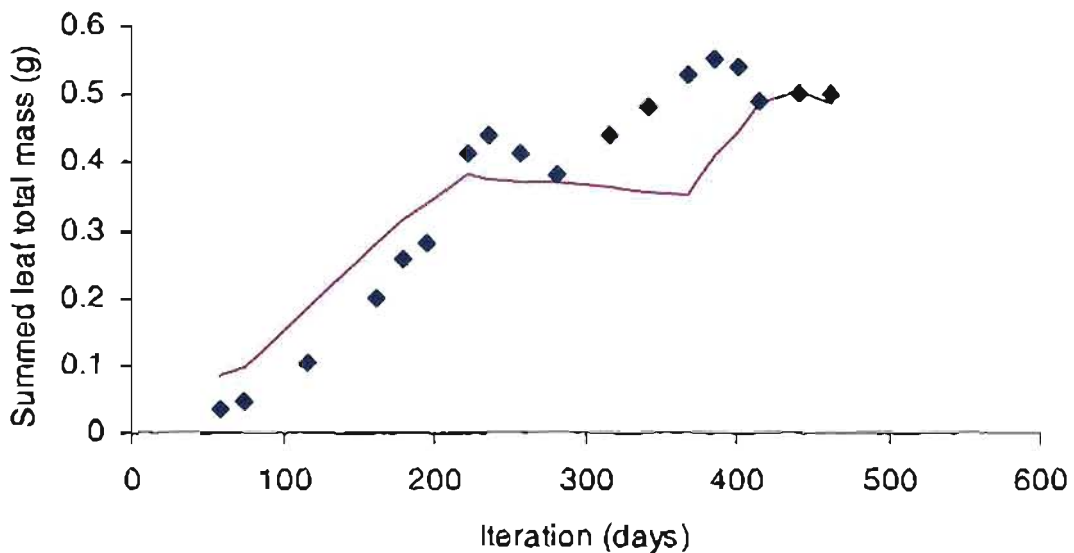

Figure 5.16   Comparison of summed leaf total mass of simulated values and empirical estimates for the years 1961-62 at Ukulinga (—— simulated; ♦ empirical). (Environmental conditions: Plant activity restricted by daily temperature and soil water pressure data for the site, as defined in Sections 4.1 and 4.2 of Chapter 4. Soil nitrogen is not limiting to growth.)
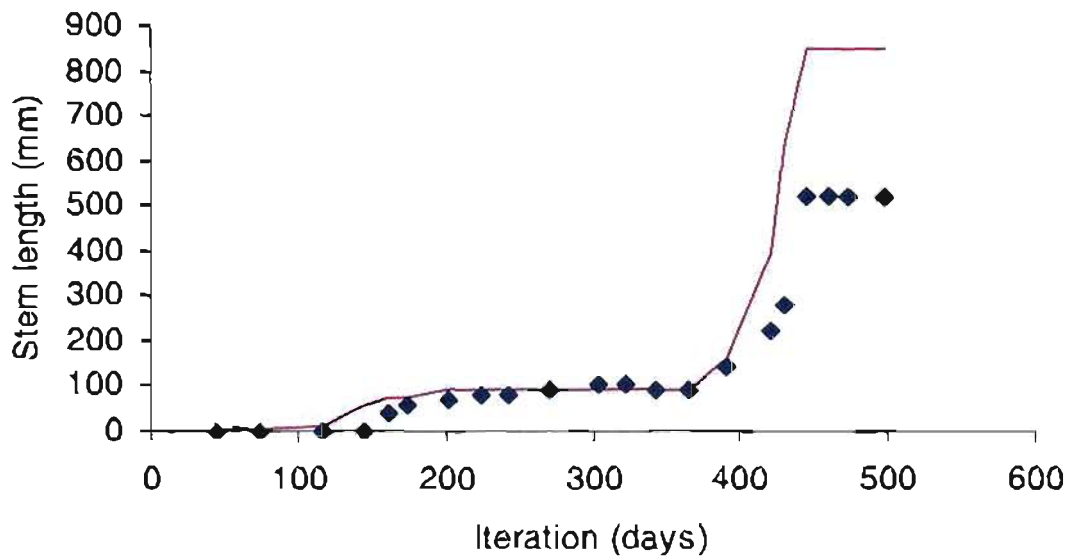
Figure 5.17   Comparison of stem length of simulated values and empirical estimates for the years 1961-62 at Ukulinga (—— simulated; ◆ empirical). (Environmental conditions: Plant activity restricted by daily temperature and soil water pressure data for the site, as defined in Sections 4.1 and 4.2 of Chapter 4. Soil nitrogen is not limiting to growth.)
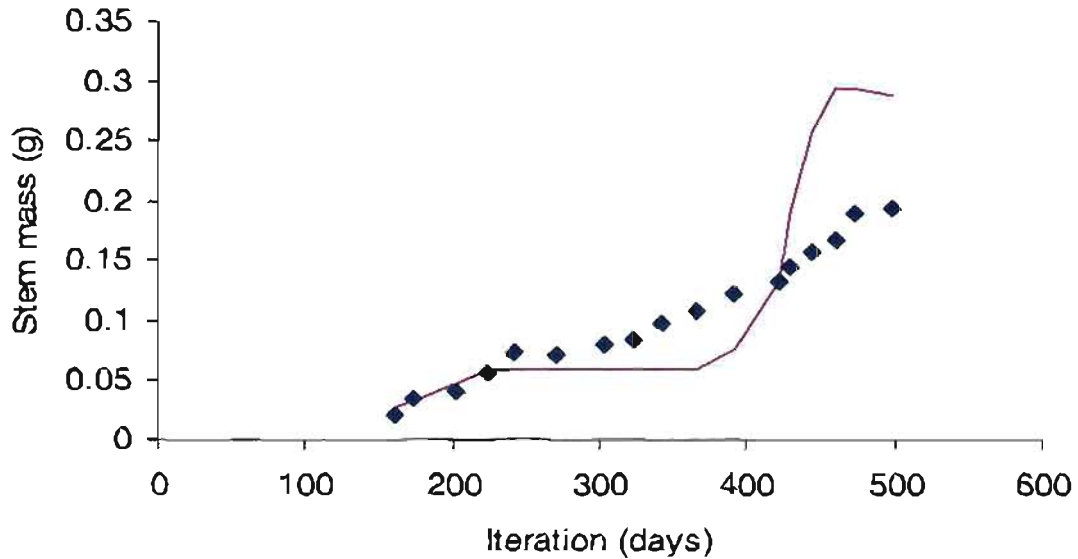
Figure 5.18   Comparison of stem mass of simulated values and empirical estimates for the years 1961-62 at Ukulinga (—— simulated; ◆ empirical). (Environmental conditions: Plant activity restricted by daily temperature and soil water pressure data for the site, as defined in Sections 4.1 and 4.2 of Chapter 4. Soil nitrogen is not limiting to growth.)

Figure 5.19 Comparison of tiller total mass of simulated values and empirical estimates for the years 1961-62 at Ukulinga (—— simulated; ♦ empirical). (Environmental conditions: Plant activity restricted by daily temperature and soil water pressure data for the site, as defined in Sections 4.1 and 4.2 of Chapter 4. Soil nitrogen is not limiting to growth.)
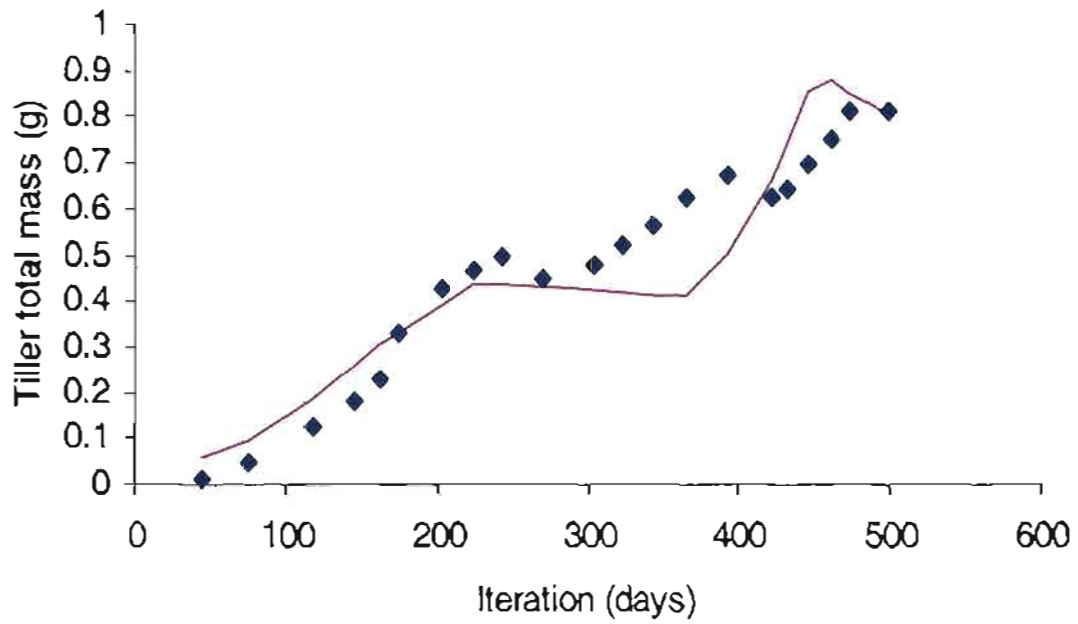
greater length simulated by the model for the reproductive phase and the increased length of time taken to achieve final length. This may in part be due to differences in the stem elevation data used to obtain the stem height, but such a large difference would suggest that water limitation may have restricted internode extension permanently. This permanent effect of water limitation on organ extension is not well-understood by the author, so I have avoided including functions to model it. It is clear that the process works at the cellular level between cellular division at the meristem and cellular expansion subsequent to this. What is important is that the model has captured the seasonal distribution of internode growth processes very well.

Table 5.2 Error analysis of the TILLERTREE model used to simulate the empirical data set of Tainton & Booysen (1965)

Variable	RMSPE (%)	MSE (units^2)	Inequality statistics		
			U^M	U^S	U^C
Summed leaf total length (mm)	0.385	40527	0.011	0.294	0.695
Summed leaf total mass (g)	0.4949	0.0063	0.083	0.395	0.522
Stem length (mm)	4.837	27541	0.321	0.619	0.060
Stem mass (g)	0.381	0.0032	0.083	0.633	0.284
Tiller total mass (g)	1.094	0.0087	0.001	0.000	0.999

Summed total leaf mass and length both have large U^C values relative to other error portions suggesting that the differences between empirical data and simulated data are due to random components not included in the model. The large hump in the empirical data during the first season (around day 230) occurred when moist conditions followed a dry period during summer. This effect could be caused by an accumulation of non-differentiated phytomers during the summer dry spell that expanded simultaneously when water conditions improved. This is a similar problem to that already mentioned for the stem length

differences during the reproductive phase. This effect is once again ignored because its effect is very small, as indicated by the small RMSPE value for the variable.

The increase in leaf mass during winter for the empirical data is strange, considering that moisture conditions were very dry, so growth was improbable. The most likely explanation is that this is a sampling anomaly arising from the small sample size employed by Tainton & Booysen (1965) (6 tillers measured at each sampling event). Therefore the fact that the model does not follow this increase during winter is considered irrelevant.

The RMSPE of tiller total mass is just over 1%, but the error is almost totally concentrated in unequal covariance (U^C). This must be seen in context. The model appears to overestimate leaf mass and underestimate stem mass at the same times and *vice versa*. This cancels some of the difference between the simulated and empirical values of tiller total mass. This partly explains why empirical and simulated estimates of this parameter are so similar at the end of flowering, because the empirical summed leaf total mass estimate is higher than the simulated value at this time, while the empirical stem mass estimate is lower than the simulated value. That said, the small size of the RMSPE for summed leaf total mass and stem mass gives us confidence that the simulated estimates for tiller total mass across time is sufficiently close to the empirical estimate not to require further adjustment.

CONCLUSION

It is apparent that the model is able to simulate the structural growth pattern of individual *Themeda triandra* tillers very well, both qualitatively in terms of the seasonal distribution of organ growth processes and quantitatively in terms of the actual values of organ mass and length predicted. It was anticipated that the model would produce reasonable results because of the low level at which values are measured, that being the organ level. The predicted success with one species suggests that the model will easily simulate growth in other tufted grasses, as long as there is sufficient data to parameterise the specific organ characteristics of the considered species.

SECTION 2

Growth of Single-Tiller Ramets

This section explores how changes in environmental resource availability interact with tiller structure and internal resource partitioning of single-tiller ramets clones. In order to do this, restrictions are introduced that both limit environmental resources and limit the ability of clones to retain unutilised resources. Secondary tiller recruitment is prevented in order to concentrate on the interactions between seasonal resource availability, tiller phenology, and resource partitioning. In doing this, behavioural complexity that may arise from the manner in which resources are allocated between connected tillers is avoided.

The first chapter in this section (Chapter 6) explores root-to-shoot partitioning. The chapter introduces a number of partitioning models, and then tests their behaviour in response to imposed dynamic resource environments.

The second chapter in this section (Chapter 7) concentrates on the problem of carbohydrate restriction during regrowth after the non-growing season, which is here termed the Spring Photosynthesis Bottleneck. This arises when tillers that have senesced their leaves over winter are forced to expand new leaves through the overlying dead canopy that substantially reduces photosynthetic potential. A number of morphological adaptations are introduced that may help bunchgrass tillers to overcome the bottleneck. These strategies are assessed, both separately and in combination with one another, in terms of the contribution they make in helping bunchgrass plants overcome the resource bottleneck.

For the remainder of the simulations in this thesis, the number of LAI layers is increased to 100 layers each of 10 mm depth. This is in order to smooth the dissipation of light and photosynthesis down the canopy.

Chapter 6:

A Co-ordinated Demand-and-Supply-Led
Root-to-Shoot Partitioning Model

Internal plant resource availability varies dynamically in response to shifts in source-sink relationships in plants (e.g. Farrar 1988). These shifts are caused by external environmental constraints on resource availability (e.g. Birch 1958; Blair *et al.* 1998; Poorter & Nagel 2000; Andrews *et al.* 2001) and growth activity (Garwood 1967; Farrar 1988), and by internal genetically-driven variables such as shifts in phenology that change the demands for resources (Trewavas 1991; Andrews *et al.* 2001) and limitation on resource storage (e.g. Farrar & Williams 1991).

The most important component to the problem and possibly the least understood is allocation of limited resources among organ types. This problem has generally been reduced to a simpler problem of allocation between shoots and roots where each component provides different resources (Thornley & Johnson 1990; Reynolds & Chen 1996; Andrews *et al.* 2001). Shoots contain the photosynthetic machinery and therefore are the source of carbohydrates, while roots source water and mineral nutrients including nitrogen from the soil. This simplification appears to be well-founded, as there is strong evidence that shifts in irradiance and soil nutrients cause consistent shifts in the root-to-shoot ratio (R:S) in plants (Poorter & Nagel 2000; Andrews *et al.* 2001).

The main difficulty with modelling root-to-shoot allocation is that we lack a mechanistic understanding of the controls over root-to-shoot allocation in plants, and can only speculate as to the controls and mechanisms involved. As a result of the lack of a clear mechanism for root-to-shoot allocation, most modelling approaches on the subject are heuristic. Most root-to-shoot partitioning models allocate to roots and shoots with reference to nitrogen (a resaource supplied by roots) and carbohydrate (a resource supplied by shoots). Three main types may be identified, namely functional balance models (e.g. Reynolds & Thornley 1982; Thornley & Johnson 1990), co-ordination models (Reynolds & Chen 1996) and transport resistance models (e.g. Thornley 1972; Thornley 1991). The functional balance models and co-ordination models are both goal-based, while the transport resistance models use a mechanistic approach to the problem.

Functional balance models use the functional balance between the supply rate of two substrates, nitrogen and carbon (e.g. Reynolds & Thornley 1982; Thornley & Johnson 1990). Generaly the objective of these models is to maintain maximum growth rates across the plant at any given time.

Co-ordination models attempt to maintain root and shoot growth in proportion to the rate at which they supply resources to the system. These co-ordination models (they co-ordinate growth of roots and shoots in order to match the available resources) behave appropriately when applied to stable environmental conditions and are able to respond fairly rapidly to sudden changes in resource availability. To date these models assume that plants grow in response to environmental resources only (supply-driven). Reynolds & Chen (1996) recognised that allocation is at least in part determined by relative demand of roots and shoots (demand-driven) which may change with development stage (Coleman, McConnaughay & Ackerly 1994), but chose to ignore this in order to simplify the presentation of their model. These problems need to be addressed when attempting to model actual seasonal growth with development stages taken into consideration.

The transport resistance models (Thornley 1972; Thornley 1991) are based on the concept that the rate of transport of carbohydrate from shoot to root and nitrogen from root to shoot respectively is proportional to the concentration gradient divided by a flow resistance. Hence if photosynthate production declines, proportionally more of the available shoot carbohydrate is allocated locally to shoot growth, and similarly if nitrogen absorption declines more of the available root nitrogen is allocated to root growth. There is evidence that transport from source sites reduces rapidly under conditions of resource deprivation and increases the relative growth of the source organs (McDonald, Ericsson & Lohammer 1986). However Andrews et al. (2001) discount the validity of transport resistance models on the basis of the following points. There is considerable evidence that transport of carbohydrate in the phloem is driven by a concentration gradient, while nitrogen transport is driven by transpiration in the xylem. In addition there is considerable data for many higher plants that the main site of NO_3^- assimilation is in the shoot (Andrews 1986). Hence the gradient/resistance model cannot apply (Andrews et al. 2001). Therefore the co-ordination models and functional balance models appear to be more appropriate for allocating nitrogen and carbon.

A major weakness of supply-driven partitioning models is that they lack proactive co-ordination between roots and shoots (e.g. Reynolds & Thornley 1982; Thornley & Johnson 1990; Reynolds & Chen 1996), and therefore rely solely on reaction to shifts in

relative internal resource availability to drive partitioning. Consequently they could potentially cause unrealistic root-to-shoot ratios under certain environmental scenarios. To illustrate this, consider humid grasslands which are severely nitrogen-restricted during the middle of summer because available soil nitrogen has been sequestered by microbes and plants by this time. If the simulated plant only grew according to the relative availability of substrate, all growth would be allocated to roots. Since phytomer blades have a limited lifespan these would finish their lifecycles and senesce, leaving the tiller with minimal photosynthetic surface before the reduced ratio of carbohydrate supply caused an increase in proportionate resource allocation to shoots once again. In reality bunchgrass tillers continue to grow live blades through summer even though root nitrogen absorption may be minimal, while internal nitrogen concentration slowly declines. In addition there is no evidence in the literature indicating such extreme seasonal shifts in root-to-shoot ratio, where roots grow while shoots do not. Hence, in the absence of any contrary evidence, it may be assumed that there must be some level of plant feedback which maintains the balance between roots and shoots and ensures that both systems are downgraded during unsuitable growth conditions and upgraded once conditions for growth improve. Therefore the allocation function should maintain a reasonable balance between live mass of roots and shoots.

It is likely that root-shoot feedback co-ordination in plants is achieved via molecular signals from roots to shoots and from shoots to roots, that increase or decrease growth activity in each component. There are a number of proposed mechanisms which involve molecules, including hormones and non-hormonal molecules such as sucrose (Van der Werf & Nagel 1996; Farrar et al. 2000). Of the hormones, it is clear that auxin is synthesised in the shoots and has a promotive effect on root growth (Cline 1994). A second hormone group, the cytokinins, is synthesised in the roots and has a strong promotive effect on cell division and tiller recruitment in the shoots (Bangerth 1989; Bangerth, Li & Gruber 2000). Plausibly their production could be manipulated by local signals in the shoots and roots respectively that reflect shifts in local resource availability (Van der Werf & Nagel 1996; Tomlinson & O'Connor 2004). The implication of this remote signal is that root growth can be moderated by shoot signals. In turn, root activity provides resources and hormones to shoots, such as NO_3^-, NH_4^+ and cytokinins which provide feedback to moderate the signal generated by the shoot. In this way the plant system can maintain functional balance through a dual feedback process.

In this chapter I introduce two variations on a new co-ordinated partitioning model for root-to-shoot allocation of carbohydrate and nitrogen resources around a plant that both

reacts to resource supply rate and proactively adjusts the relative demands placed by roots and shoots based on the relative deficits of the two resources. The behaviours of the two variations of the co-ordination model are compared to a fixed partitioning model (described below) using simple simulations that change environmental availability of light (necessary to manufacture carbohydrates) and soil nitrogen.

1   TWO CO-ORDINATED PARTITIONING MODELS

1.1   A co-ordinated demand-led partitioning model

In this co-ordination model I seek to incorporate the growth demands of each component. The manner in which roots can rapidly divide and subdivide means that their potential relative growth in each iteration could be large relative to potential shoot growth. Therefore their potential to outgrow shoots is vast since the latter have very strict rules for secondary tiller recruitment that substantially inhibit recruitment under natural environmental conditions (Tomlinson & O'Connor 2004).

Disproportionate partitioning of growth resources between shoots and roots is achieved by adjusting the relative growth demands placed by each component. Therefore the model can be said to use demand-led resource partitioning. Shoot growth in the TILLERTREE model is fixed by the pre-defined growth of individual shoot organs (described in Chapter 2). Root growth is calculated using a goal-gap formulation based on the difference between actual root-to-shoot ratio and the ideal root-to-shoot ratio, $\Omega alrlsh_{y,\delta,t}$. The potential daily root growth, $\Psi gwlr_{y,t}$, is determined by the size of the gap between the actual and the ideal root-to-shoot ratio, and the maximum rate at which roots can grow in a single iteration, which depends on the size of the root and the potential daily root growth rate ($maxgwlr_i$).

$$\Psi gwlr_{y,t} = min\left(max\,gwlr_i\,wlr_{y,t-1} \quad ; \quad \Omega alrlsh_{y,t}\,wlsh_{y,t-1} - \frac{wlr_{y,t-1}}{wlsh_{y,t-1}} \right). \quad \textbf{6.1}$$

If the ideal root-to-shoot ratio is fixed, then the relative resource demand for growth placed by roots to that placed by shoots will remain fixed across iterations, and is called a fixed

partitioning model. Any changes to the ideal root-to-shoot ratio, $\Omega alrlsh_{\gamma,t}$, will adjust the proportion of resources allocated to shoots and roots respectively. Therefore changes in root-to-shoot allocation desired in response to shifts in relative nitrogen and carbohydrate resource availability can be achieved simply by adjusting the value of $\Omega alrlsh_{\gamma,t}$.

The value of $\Omega alrlsh_{\gamma,t}$ is bound between a minimum root-to-shoot ratio ($minalrlsh_i$) and a maximum root-to-shoot ratio ($maxalrlsh_i$) respectively. It is assumed that these values are maintained by the co-ordination signals between roots and shoots. If both nitrogen and carbohydrate resources are non-limiting to growth, then the value taken by the $\Omega alrlsh_{\gamma,t}$ is the mid-point between the maximum and minimum root-to-shoot ratios ($midalrlsh_i$). If either carbon or nitrogen is limiting to growth then the $\Omega alrlsh_{\gamma,t}$ is moved away from the mid-point value by the direction and magnitude of the resource imbalance ($Imbalance_{\gamma,t}$).

$$\Omega alrlsh_{\gamma,t} = midalrlsh_i - imbalance_{\gamma,t} \left(\frac{\min alrlsh_i - \max alrlsh_i}{2} \right).$$
6. 2

There are two advantages to bounding the ideal root-to-shoot ratio. Firstly the bounds ensure that growth is downgraded in both roots and shoots when one resource is severely restricted and therefore can be used to prevent unrealistic root-to-shoot ratios while ensuring an appropriate growth response when the root-to-shoot ratio is severely skewed by defoliation events. Secondly, it is probable that a reasonable estimate of $minalrlsh_i$ and $maxalrlsh_i$ could be obtained empirically through careful resource-supply experiments. This means that if root-to-shoot partitioning is a property of individual species it can easily be changed in the model.

A delay in the root growth adjustment is introduced using a moving average of the ideal root-to-shoot ratio averaged over the last five days.

$$\Omega alrlsh_{\gamma,t} = \frac{1}{5} \sum_{t-4}^{t} \Omega alrlsh_{\gamma,t}$$
6.3

The imbalance function calculates the relative insufficiency of each resource (AVC, AVN) to the absolute growth demand for that resource ($CDemGrow_{\gamma,t}$, $NDemGrow_{\gamma,t}$) (also see Reynolds & Chen 1996).

$imbalance_{\gamma,t} =$

$$
\begin{cases}
1 & \text{if } \left[(AVN_{\gamma,t} \geq NDemGrow_{\gamma,t}) \text{ AND } (AVC_{\gamma,t} \geq CDemGrow_{\gamma,t})\right], \\[2mm]
\dfrac{AVN_{\gamma,t}}{NDemGrow_{\gamma,t}} - 1 & \\
& \text{if } \left[(AVN_{\gamma,t} < NDemGrow_{\gamma,t}) \text{ AND } (AVC_{\gamma,t} \geq CDemGrow_{\gamma,t})\right], \\[2mm]
1 - \dfrac{AVC_{\gamma,t}}{CDemGrow_{\gamma,t}} & \\
& \text{if } \left[(AVN_{\gamma,t} \geq NDemGrow_{\gamma,t}) \text{ AND } (AVC_{\gamma,t} < CDemGrow_{\gamma,t})\right], \\[2mm]
\dfrac{AVN_{\gamma,t}}{NDemGrow_{\gamma,t}} - \dfrac{AVC_{\gamma,t}}{CDemGrow_{\gamma,t}} & \text{otherwise}.
\end{cases}
$$

<div align="right">6. 4</div>

Negative values of imbalance$_{\gamma,t}$ mean nitrogen is more restrictive than carbohydrate, so the relative demand of roots will increase. Positive values of imbalance$_{\gamma,t}$ mean carbohydrate is more restrictive than nitrogen, so the relative demand of roots will decrease. If both resources are highly restricted the function will not fail because the imbalance is calculated by difference and not by division of relative availability. If either resource exceeds the total growth demand, then that fraction is set equal to 1. This is necessary to ensure that shifts in the ratio are based on resource insufficiency and not on the difference in availability between the two resources. Consequently:

$$-1 \leq imbalance_{\gamma,t} \leq 1.$$

<div align="right">6. 5</div>

1.2 Extension to a co-ordinated dual demand-and-supply-led partitioning model

The model presented in the previous section describes a feedback model that moderates the relative growth demand placed by roots and shoots. However it ignores daily movements in resources that result from resource limitation in the plant. That is, it is important to recognise that movement of resources from source to sink is affected by the resource demands of the source organ. If resource productivity is limiting then it is reasonable to assume that relatively more of the available resource will be utilised by the source organ

simply because of its proximity to the site of production or acquisition. This behaviour is simulated by the mechanisms in the transport resistance models (Thornley 1972; Thornley 1991). For the present model, it may be incorporated by recognising that there is a bias at each iteration in the allocation of resources between source organs and sink organs of a given resource.

Therefore a function was introduced that would manipulate the daily allocation of resources to shoots ($\lambda_{sh,\gamma,t}$) and roots ($\lambda_{rt,\gamma,t}$) in response to the ratios of daily carbohydrate and nitrogen demands for growth relative to daily AVN and AVC after maintenance carbohydrate and Cstore$_{\gamma,\delta,t}$ had been satisfied. This extension mimics the supply-led co-ordination model of Reynolds & Chen (1996). This daily allocation function also uses the imbalance$_{\gamma,t}$ to co-ordinate resource partitioning. The imbalance$_{\gamma,t}$ assigns the value of $\lambda_{sh,\gamma,t}$ by shifting it away from 0.5.

$$\lambda_{sh,\gamma,t} = 0.5 + \frac{imbalance_{\gamma,t}}{2}.$$ 6.6

Now a proportion of the available resources, determined by the most limiting resource, can be assigned to shoot growth and root growth.

$$CShGrow_{\gamma,t} = \lambda_{sh,\gamma} \, AVC_{\gamma,t} \, \min\left[\frac{AVC_{\gamma,t}}{CDemGrow_{\gamma,t}}; \frac{AVN_{\gamma,t}}{NDemGrow_{\gamma,t}}\right].$$ 6.7

$$CRtGrow_{\gamma,t} = AVC_{\gamma,t} \, \min\left[\frac{AVC_{\gamma,t}}{CDemGrow_{\gamma,t}}; \frac{AVN_{\gamma,t}}{NDemGrow_{\gamma,t}}\right] - CShGrow_{\gamma,t}.$$ 6.8

This correction is designed to mimic the effect of increased nutrient usage by the source organs when one nutrient is more limited.

85

2   SIMULATIONS

Two simulations were conducted using the three resource partitioning models (fixed, demand-led, and dual demand-and-supply-led). The first simulation imposed carbohydrate limitation on growth by restricting carbohydrate retention. The second additionally imposed nitrogen limitation by restricting soil nitrogen availability.

The behaviour of the model was assessed by observing the growth of the model species *Themeda triandra* to critical seasonal environmental events that occur in the Southern Tall Grassveld, a humid grassland type found in KwaZulu-Natal, South Africa.

There are few estimates for the value of the root-to-shoot ratio of *Themeda triandra*. In a defoliation pot trial of the species, Coughenour *et al.* (1985) recorded yield estimates for shoot and root that gave root-to-shoot ratios of 0.83 and 1.12 for high and low nitrogen supply and 1.50 to 1.08 for no clipping and 3 cm height clipping respectively. A recent pot trial which looked at the effect of different fertilisers on growth of *Themeda triandra* found root-to-shoot ratio values that ranged between 0.53 and 1.79 for (Webb 2004). Therefore estimates of 0.5 for $minalrlsh_i$ and 1.8 for $maxalrlsh_i$ were assumed. Consequently the fixed partitioning model maintained an ideal root-to-shoot ratio of 1.15.

The following assumptions were made:

a.   *An initial amount of carbohydrate and nitrogen must be supplied to the model to start growth*

This matches natural conditions where a new tiller on a bunchgrass would be recruited off a parent tiller that supplies it with resources during the early stages of growth. The initial carbohydrate StartAVC is 0.1 g and the initial nitrogen StartAVN is 0.03 g. The order of magnitude difference between the two values reflects the difference in the relative amounts of each resource required for structural growth.

b.   *Available carbohydrate (AVC) concentration is restricted to 10% by live mass*

There is strong evidence that grasses hold at most 10% non-structural carbohydrate by live vegetative mass (Bartholomew 1968; Steinke & Booysen 1968; Danckwerts 1984; Farrar & Williams 1991). Any excess carbohydrate on this concentration level after all deductions in a particular iteration (day) is removed from the system on the assumption that it is converted to secondary metabolites.

86

c.   Available nitrogen (AVN) concentration is unrestricted

Nitrogen accumulation from the soil is very small, so net concentrations of nitrogen in plants never accumulate very greatly. Therefore it was felt unnecessary to restrict concentrations of this resource.

d.   Plants are unable to delay growth processes if resources are restricted during active growing periods.

If either nitrogen or carbohydrate is restricted, the plant is unable to delay expansion until resource availability improves.

2.1   Simulation 1 - Carbohydrate restriction, no nitrogen restriction

Carbohydrate limitation arises because of seasonal shifts in photosynthetic productivity and limitation on carbohydrate storage. Photosynthesis is limited by light attenuation through the canopy (Chapter 3). The light environment is set by the shoot structure, which is defined by the growth behaviour of the considered species.

The environment was separated into two periods, a growing season and a non-growing season. Plant activity (photosynthesis, growth, maintenance, senescence) was set at maximum rates during the growing season. During the non-growing season, growth and photosynthesis were inhibited and maintenance was reduced to 0.1 of its growing season value in order for turnover processes to proceed. Blade dieback proceeded during winter on all live blades except the youngest blade, which survived the winter period intact. This assumption was based on the observation that *Themeda triandra* tillers in the Southern Tall Grassveld maintain at least one live blade during winter (personal observation).

As the model is not horizontally explicit, plant matter density must be specified to determine light reduction through the canopy. Leaf area index (LAI) is moderated by the ground surface area parameter (GSA), which increases or decreases LAI as it is decreased or increased respectively, providing the means to observe the effect of high LAI versus low LAI on plant growth. For the present model GSA = $20.00 \, \text{cm}^2$. This gave a LAI of $3.07 \, \text{m} \, \text{m}^{-1}$ at the start of spring, which is similar to empirical estimates for a non-defoliated sward at Ukulinga (see Appendix A1).

A winter mow defoliation event was applied on day 360 just prior to start of the growing season in order to prevent carbohydrate starvation during the spring regrowth period, which occurs if the overlying canopy severely restricts photosynthetic production (this problem is explored in the next chapter). The mow was applied at a height of 8 cm above the ground to ensure that it exceeded the height of the apical meristem during the early spring period and therefore could not decapitate the tiller and terminate its growth.

For this simulation, nitrogen was non-restrictive so that all resource allocation shifts related to carbohydrate limitation alone.

2.2   Simulation 2 - Carbohydrate and nitrogen restriction

In the second simulation, the same rules were applied as for Simulation 1. In addition a restriction was placed on environmental nitrogen availability.

Maximum nitrogen absorption rate pre unit root mass, RNuptake, was set at 0.001 g N $(g \, wlr)^{-1} \, d^{-1}$. The model assumed that soil nitrogen is at maximum values during the spring period up until the end of November. Soil nitrogen availability declines linearly through November to zero, where it remains for the remainder of the growing season (Figure 4.1, Chapter 4). The initial nitrogen used to start the simulation (StartAVN), was set at 0.005 g. This value was sufficiently low to ensure that the seasonal availability of soil nitrogen would be limiting to the single-tiller ramet at certain stages in its growth because the total amount of nitrogen available was less than the integral of daily nitrogen required for unrestricted growth during the lifetime of a single-tiller ramet.

3   RESULTS

3.1   Carbohydrate restriction, no nitrogen restriction

3.1.1   Fixed-partitioning model

The results of a simulation run with the fixed partitioning model indicated that non-structural carbohydrate was sufficient throughout the first vegetative growth season (Figures

6.1 and 6.2). However carbohydrate was severely limiting at the start of spring regrowth in the second season and appeared to remain so throughout the reproductive growth phase.

No photosynthesis occurred during the first few days of the second spring because the single live blade that survived winter was very small and was covered by overlying sheaths of earlier phytomers. New growth therefore relied on carbohydrate allocation from storage, which rapidly depleted that resource. The carbohydrate limitation during early spring reduced the blade extension on the new phytomers, which restricted the subsequent photosynthetic ability of these organs. This in turn reduced the subsequent growth of both shoot and root organs. Stem growth reached a maximum length of only 345.7 mm and flower mass attained a live biomass of 0.03 g (Figure 6.3).

3.1.2 Comparison of the two co-ordinated partitioning models with the fixed partitioning model

Second season growth data, as presented in Table 6.1 below, indicates that plant growth during the second spring was improved by the two co-ordination models over the fixed model, with the dual demand-and-supply-led partitioning model accumulating greater mass than the demand-led partitioning model.

The improvement of the performance of the two co-ordination models over the performance of the fixed model was achieved because a greater portion of the growth resources were allocated to shoot growth than to root growth during early spring, which improved the growth of photosynthetic structures. This increased the photosynthetic machinery of the single-tiller ramets of the two co-ordination models, which in turn increased the photosynthetic production later in the second season, when roots received a greater portion of the available carbohydrate thereby increasing overall plant growth (Figure 6.4).
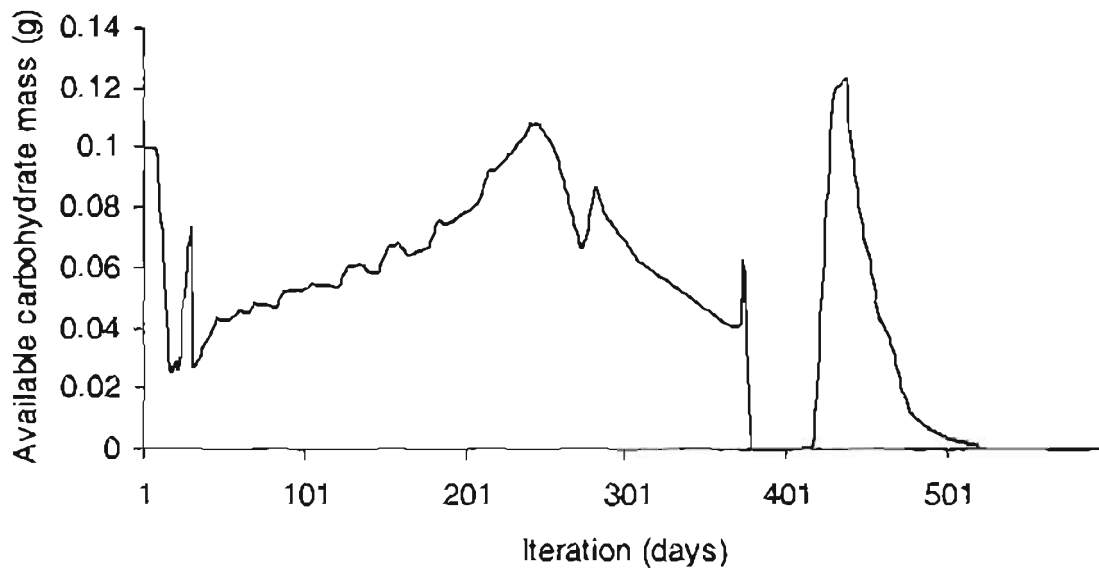
Figure 6.1   The effect of carbohydrate storage restriction on the daily available non-structural carbohydrate (AVC) of a single-tiller ramet subjected to a late winter mow of height 8 cm on day 360. Resource partitioning to roots and shoots is fixed. Nitrogen is non-limiting. (Environmental conditions: Plant activity during the growing and non-growing season as defined in Section 4.3 of Chapter 4. Growing season proceeds from Yearday 1 to Yearday 242 of each year.)
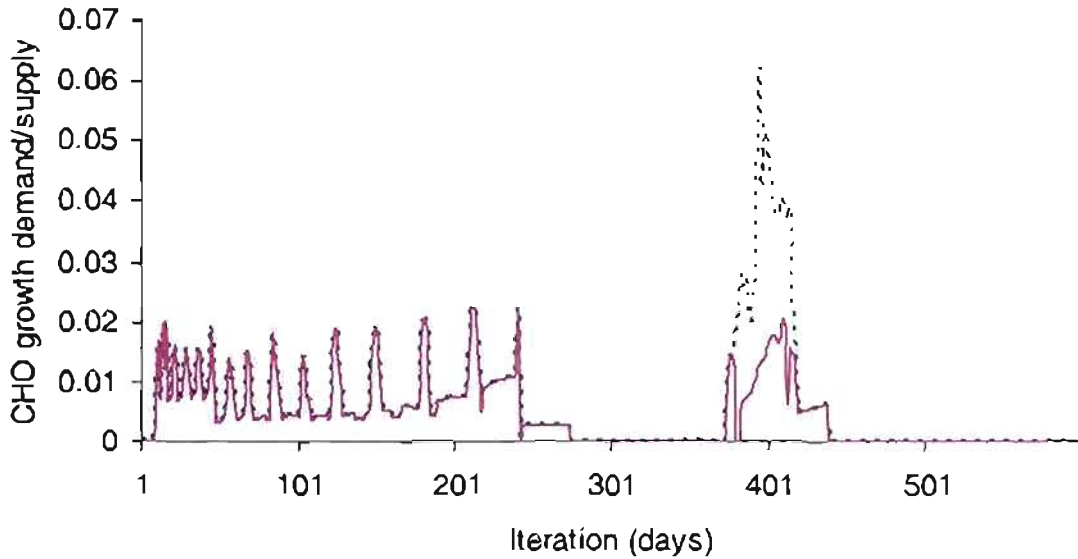
Figure 6.2   The effect of carbohydrate storage restriction on the daily carbohydrate demanded (········) and supplied (————) for growth of a single-tiller ramet subjected to a late winter mow of height 8 cm on day 360. Resource partitioning to roots and shoots is fixed. Nitrogen is non-limiting. (Environmental conditions: Plant activity during the growing and non-growing season as defined in Section 4.3 of Chapter 4. Growing season proceeds from Yearday 1 to Yearday 242 of each year.)
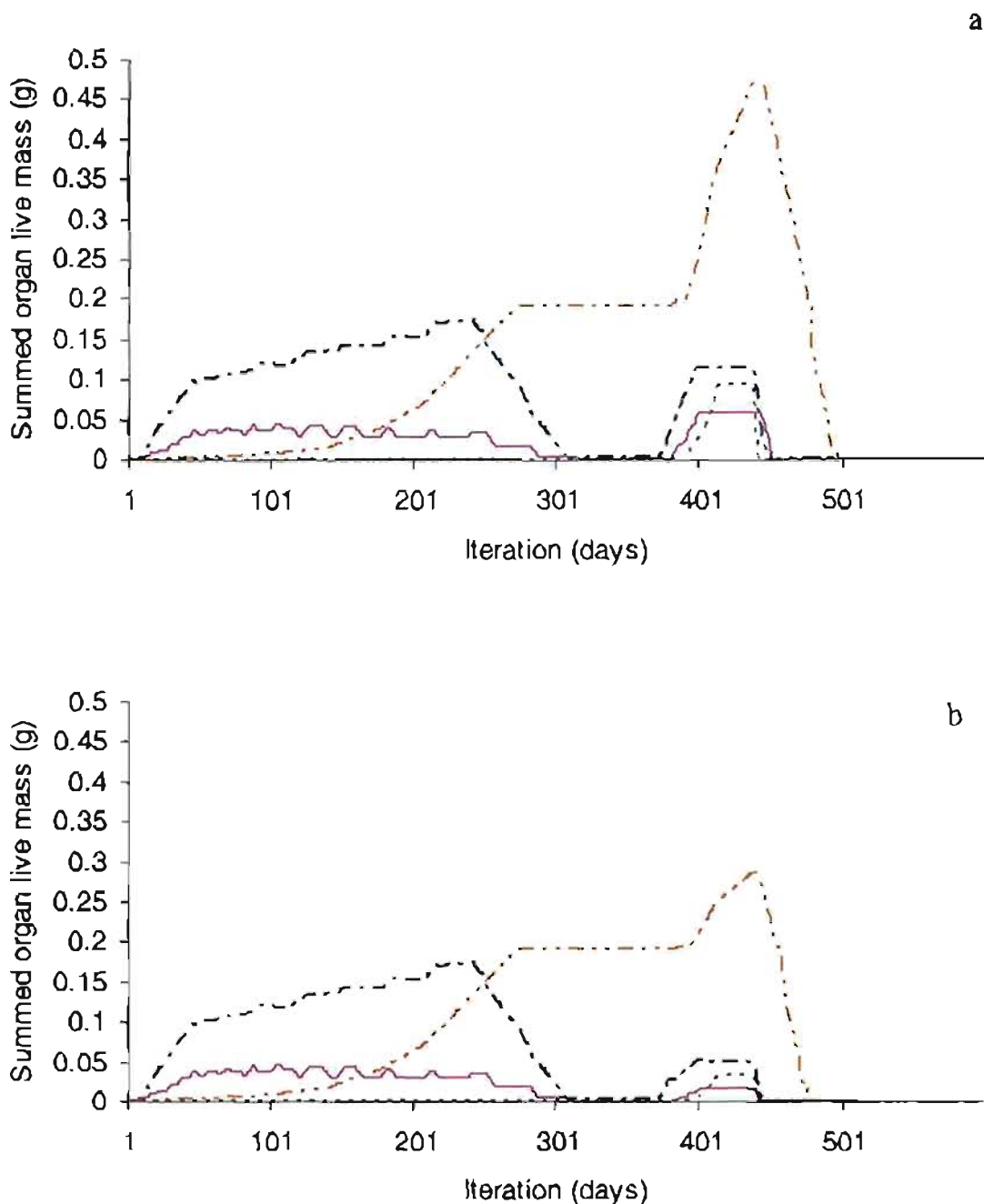
Figure 6.3 Comparison of summed live mass of shoot organs of a single-tiller ramet without carbohydrate restriction (a) and with restriction on carbohydrate storage (b). The ramet has been subjected to a late winter mow of height 8 cm on day 360. Resource partitioning to roots and shoots is fixed. Nitrogen is non-limiting. Summed live mass of organ types (— · — blade mass; ———— sheath mass; — ·· — internode mass; — — — flower mass) of a ramet with a single tiller subjected to a cutting treatment. (Environmental conditions: Plant activity during the growing and non-growing season as defined in Section 4.3 of Chapter 4. Growing season proceeds from Yearday 1 to Yearday 242 of each year.)

Figure 6.4 Live root mass (————) and live shoot mass (— — —) of a single-tiller ramet with restricted AVC storage subjected to a late winter mow, for the three partitioning models. a. Fixed partitioning; b. Demand-led partitioning c. Demand-and-resource-led partitioning. (Defoliation: height 8 cm on day 360.) Nitrogen is non-limiting. (Environmental conditions: Plant activity during the growing and non-growing season as defined in Section 4.3 of Chapter 4. Growing season proceeds from Yearday 1 to Yearday 242 of each year.)
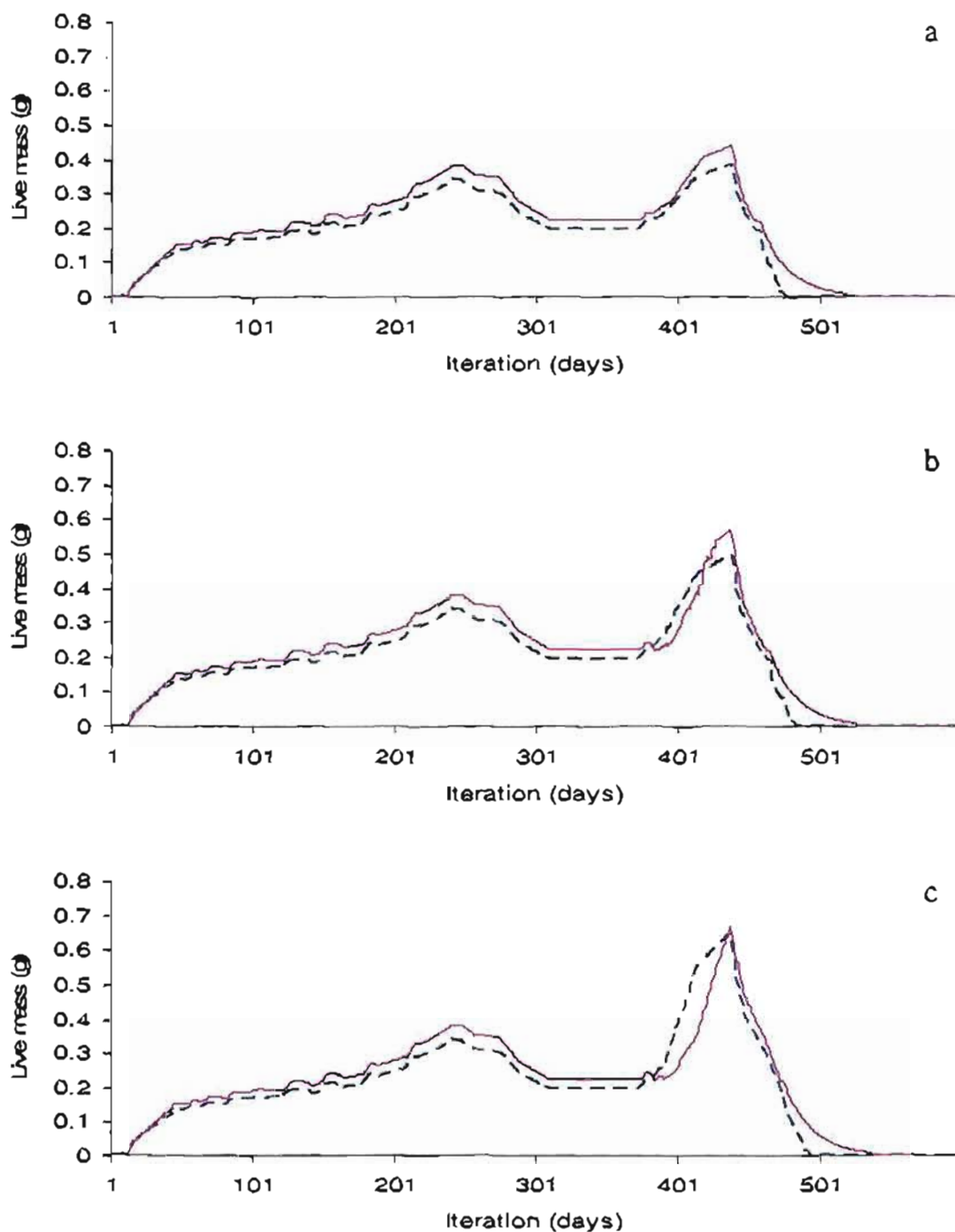
Table 6.1   The maximum live mass of organs and shoots and roots generated during the reproductive phase by each of the partitioning models

Component	Unrestricted growth*	Partitioning model		
		Fixed	Demand-led	Demand-and-supply-led
Shoot (g)	0.690	0.383	0.500	0.647
Root (g)	0.786	0.438	0.570	0.664
Blade (g)	0.115	0.049	0.070	0.083
Sheath (g)	0.062	0.016	0.031	0.040
Intenode (g)	0.421	0.277	0.341	0.441
Inflorescence (g)	0.092	0.033	0.049	0.083
Culm length (mm)	794.58	345.68	520.85	737.77

* potential growth of single-tiller ramet using a fixed partitioning function, without resource limitation

The imbalance functions and the ideal and actual root-to-shoot ratios generated by each partitioning model are shown (Figures 6.5 and 6.6). The imbalance function of the fixed partitioning model of course does not affect partitioning, but it does help illustrate the effect of the two co-ordination models. The imbalance function of the fixed partitioning model is continuously positively skewed during the growth period in the second season indicating that carbohydrate is continuously limited during this time in this model. By contrast the demand-led partitioning model has many days where carbohydrate is not limiting to growth, indicating that the feedback reduction on root growth demand has a beneficial effect by reducing the integral of daily imbalance in spring. The dual demand-and-supply-led partitioning model has a longer period of continuous resource imbalance which results from the daily allocation of proportionately more resources to shoots on the basis of the resource imbalance. This reduces the actual root-to-shoot ratio further below the ideal root-to-shoot ratio than occurs with the demand-led partitioning model. However this strategy increases the blade growth in early spring over the demand-led partitioning model which ensures more photosynthesis for greater shoot and root growth later in the spring.
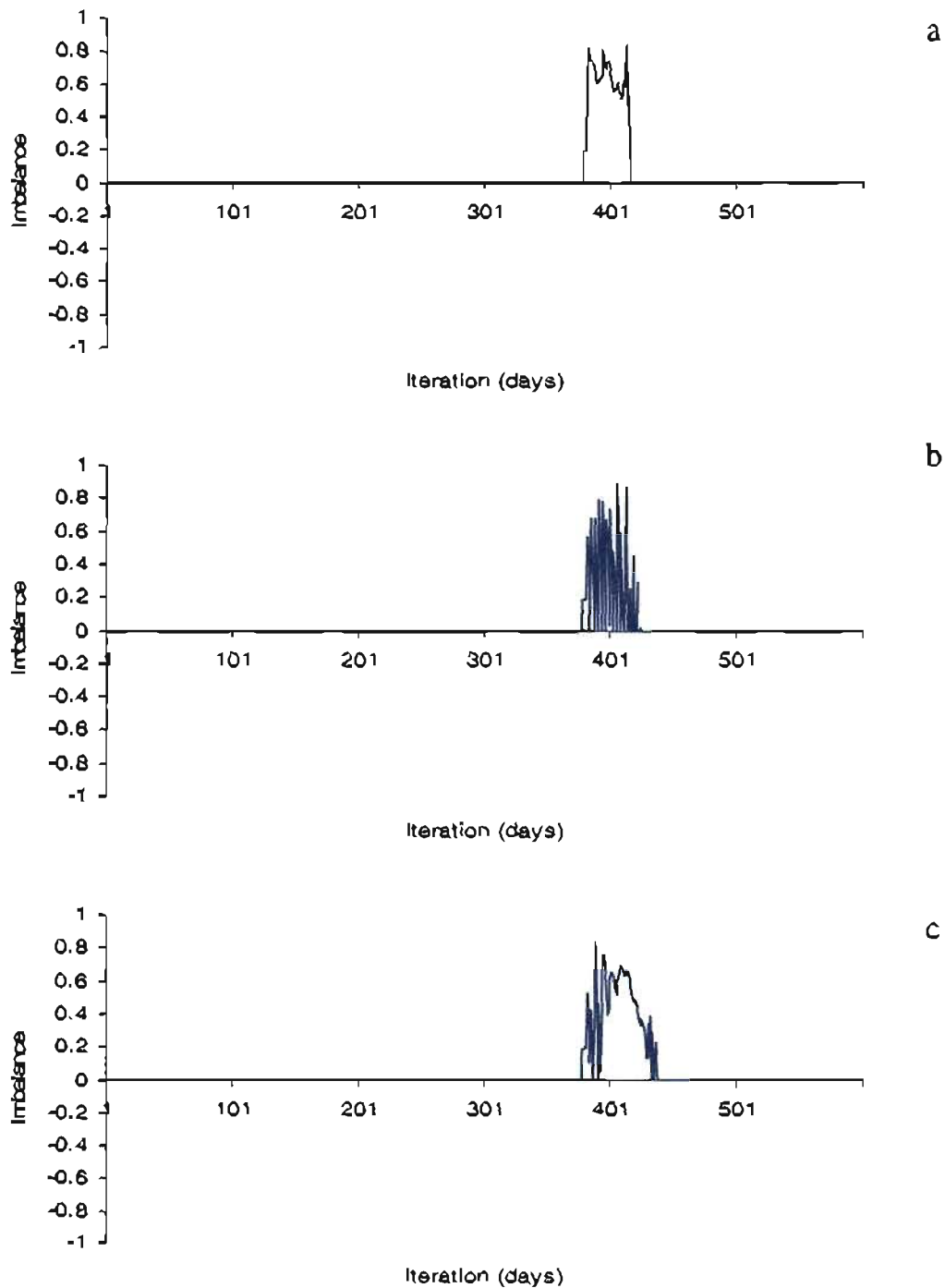
Figure 6.5   Response of the imbalance function to restriction on AVC storage of a single-tiller ramet subjected to a late winter mow, for the three partitioning models. a. Fixed partitioning; b. Demand-led partitioning c. Demand-and-resource-led partitioning. (Defoliation: height 8 cm on day 360.) Nitrogen is non-limiting. (Environmental conditions: Plant activity during the growing and non-growing season as defined in Section 4.3 of Chapter 4. Growing season proceeds from Yearday 1 to Yearday 242 of each year.)
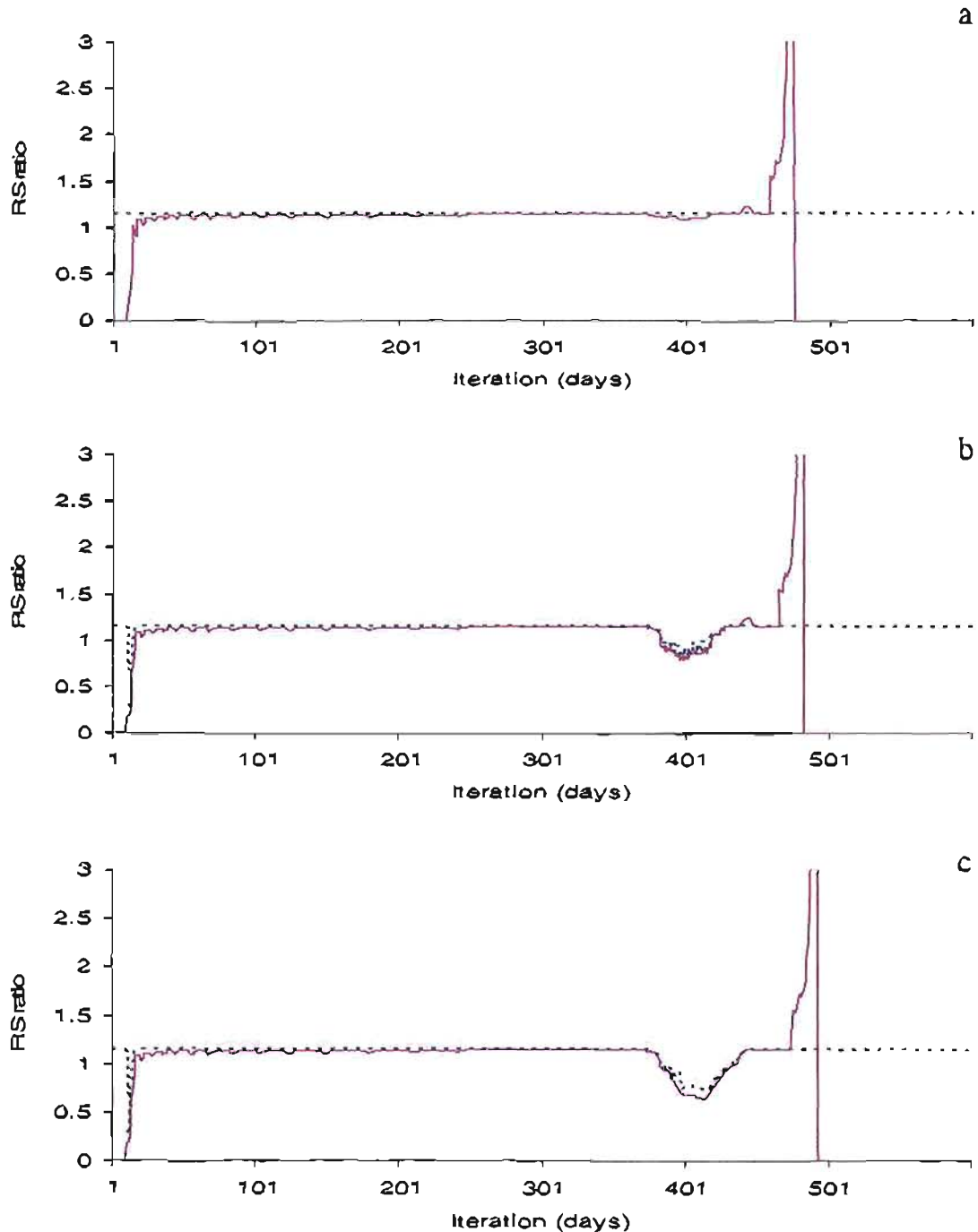
Figure 6.6   Response of the actual R:S ratio (———— αlrlsh$_{\gamma,\delta,t}$) and ideal R:S ratio (········ $\Omega\alpha$lrlsh$_{\gamma,\delta,t}$) to restriction on AVC storage of a single-tiller ramet subjected to a late winter mow, for the three partitioning models. a. Fixed partitioning; b. Demand-led partitioning c. Demand-and-resource-led partitioning. (Defoliation: height 8 cm on day 360.) Nitrogen is non-limiting. (Environmental conditions: Plant activity during the growing and non-growing season as defined in Section 4.3 of Chapter 4. Growing season proceeds from Yearday 1 to Yearday 242 of each year.)

All three models are able to achieve non-restricted growth before the end of the reproductive growth phase. The fixed partitioning model achieves this first, followed by the demand-led partitioning model and then the dual demand-and-supply-led partitioning model respectively.

Immediately post the start of spring regrowth, both roots and shoots grow for a few days under all three partitioning strategies (Figure 6.4). This indicates that the release of carbohydrate from stored sources ensures that there is no imbalance in the resources at this time. This is because the carbohydrate storage function releases up to 67 % of its resources into AVC in a single day. Therefore the available carbohydrate for growth at the start of spring exceeds daily demands. This increased concentration is probably not realistic, and the net effect is that some carbohydrate is allocated to roots by the imbalance function that could potentially be better utilised in shoots if the amount of carbohydrate released from storage was slower.

3.2 Nitrogen restriction

Data on the behaviour for the partitioning models in response to the additional restriction on N availability is only given for the dual demand-and-supply-led partitioning model.

The effect of the restrictions on initial nitrogen supplied and nitrogen absorbed through the season indicate that AVN is limited during autumn of the first season and during the first winter (Figure 6.7). The AVN is restricted during autumn because there is no nitrogen absorption during this period. The imbalance function has two narrow troughs during the autumn period (Figure 6.8), which indicate that nitrogen is more limiting to growth than carbohydrate at this time. The two troughs in imbalance coincide with the expansion of blades on new phytomers. Imbalance returns to zero in between these demand peaks because the growth demand is much reduced between phytomer expansions. However growth demand never declines to zero during the autumn period, so AVN was at zero at the end of each cycle because of the nitrogen remaining in it after growth was allocated to Nstorage (Figure 6.7). The demand placed by Nstorage also explains why AVN was at zero during the winter period.

The imbalance function increased proportional allocation to roots during the first autumn (Figure 6.8). However in the second spring growth was still more severely limited by carbohydrate than nitrogen. Therefore the imbalance function was strictly positive during

91
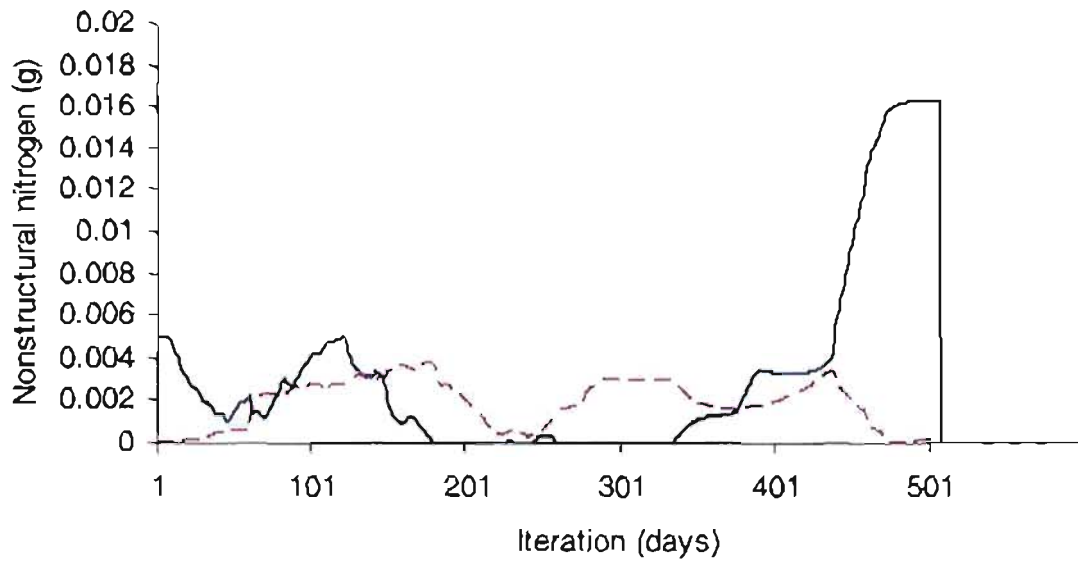
Figure 6.7 The effect of the seasonal daily nitrogen absorption function and the initial N used to initiate the simulation (StartN = 0.005 g) and the growth pattern of the single-tiller ramet on the non-structural nitrogen content (———— AVN; — — — — Nstorage) of the ramet. Daily soil nitrogen availability as described in Section 3 of Chapter 4. (Environmental conditions: Plant activity during the growing and non-growing season as defined in Section 4.3 of Chapter 4. Growing season proceeds from Yearday 1 to Yearday 242 of each year.)
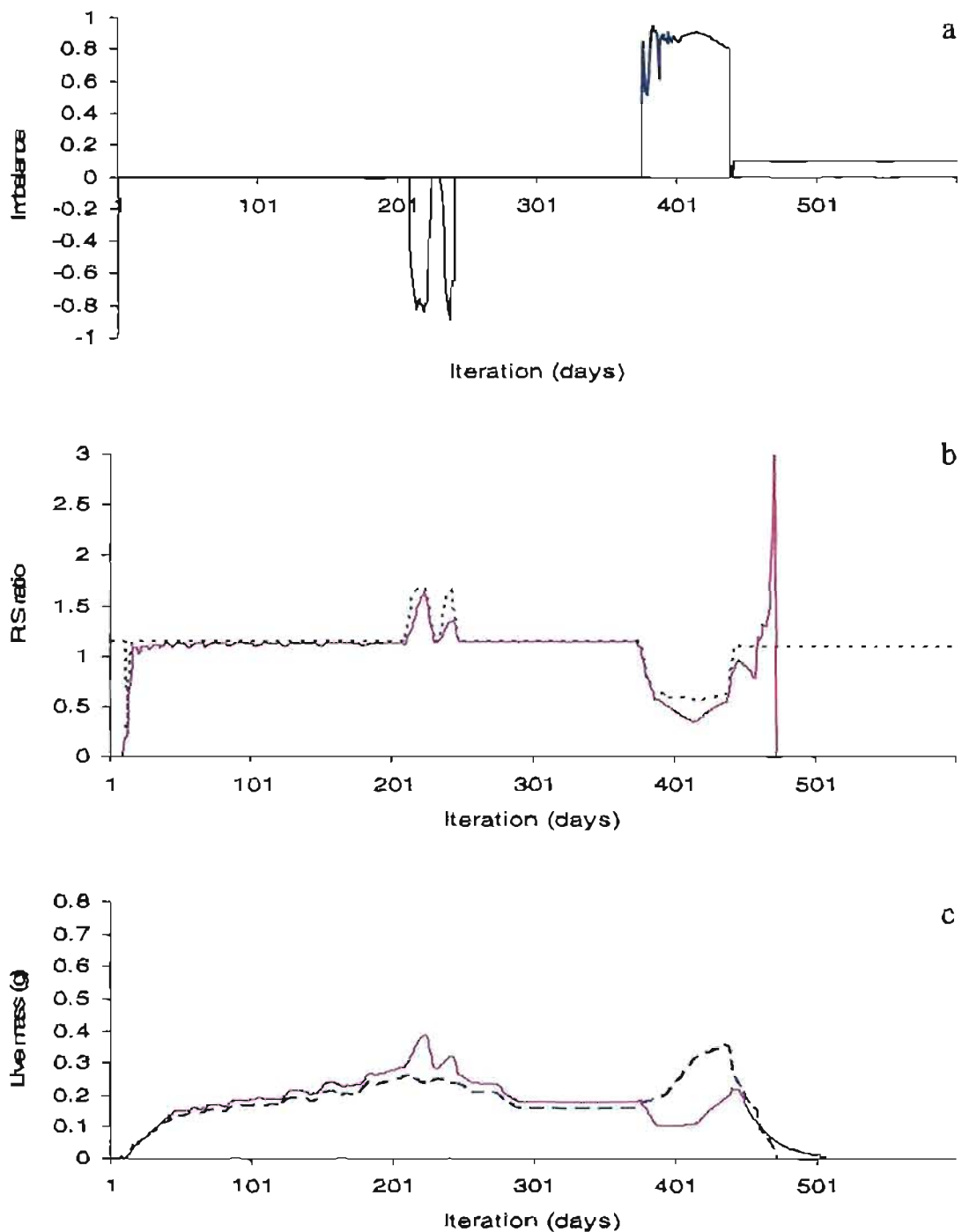
Figure 6.8 The effect of combined N limitation and carbohydrate limitation on: a. The imbalance function. b. Ideal and actual root to shoot ratios (·········· $\Omega\alpha lrlsh_{\gamma,\delta,t}$, and $\alpha lrlsh_{\gamma,\delta,t}$ ————, respectively). c. Actual live root mass (————) and live shoot mass (— — —). Daily soil nitrogen availability as described in Section 3 of Chapter 4. (Environmental conditions: Plant activity during the growing and non-growing season as defined in Section 4.3 of Chapter 4. Growing season proceeds from Yearday 1 to Yearday 242 of each year.)

this period. This reflected a reduction in stored carbohydrate because the size of the tillers was smaller over winter due to the restriction of growth during winter. This reduction of carbohydrate availability reduced the amount of early spring blade growth, which in turn reduced carbohydrate production later in the second spring. The imbalance function induced substantial dieback of roots during spring in order to allow more resources to be allocated to shoots. However this did not overcome the main problem, which was that there was too little carbohydrate stored during winter to overcome the demand deficit that developed during the early part of spring regrowth. Clearly carbohydrate limitation during spring regrowth is a critical hurdle for grass plants to overcome. This problem is dealt with in the next chapter.

4   DISCUSSION

The dual demand-and-supply-led partitioning model presented here uses two signals of control, relative growth demand from shoots and roots and daily relative resource/demand imbalance (supply). The relative growth demand of shoots and roots is a medium-term response to shifts in relative nitrogen and carbon resource availability. It mimics the effect of signals from roots to shoots and from shoots to roots that adjust the relative growth demand in response to relative nutrient availability (Van der Werf & Nagel 1996; Bangerth et al. 2000; Farrar & Jones 2000). The daily allocation in response to actual imbalance reflects more immediate shifts in resource allocation that increases growth of the organs that source the more limiting nutrient (McDonald et al. 1986; Van der Werf & Nagel 1996).

The model assumes that growth activity is co-ordinated both by shoot phenology (Cheng, Coleman & Box 1990) and internal resource availability (Andrews et al. 2001). This assumption is not unreasonable, as shoot structures serve multiple purposes that change in time (photosynthesis, sexual reproduction, and vegetative reproduction in clonal plants) and consequently change growth demands, while roots serve two unchanging purposes, nutrient resource capture and plant anchorage to the substrate.

A key advantage of this method is that it upgrades or downgrades relative root and shoot growth activity proactively in response to resource availability. This allows the plant to adapt its relative resource demands. This is a fundamental change from previous models where daily demands placed by roots and shoots are determined by a fixed relative growth

rate, and allocation is based on the imbalance in internal resource availability only (Thornley & Johnson 1990; Reynolds & Chen 1996). As pointed out in the introduction supply-led partitioning alone can potentially lead to unrealistic root-to-shoot ratios when availability of one of the two resources is extremely restricted. This problem is important in grassland environments where soil nitrogen availability is both seasonal (Blair et al. 1998) and temporally-limited by soil water availability (Birch 1958). During low soil nitrogen periods, supply-led partitioning would cause plants to tend to unrealistically large root-to-shoot ratios, because supply-led co-ordination models respond to internal resource deficits by increasing resource allocation to the organ that supplies the more limiting nutrient. The increased absolute root growth during nitrogen-poor periods under supply-led partitioning increases resource wastage because there is a small probability of increasing nitrogen supply rate as the availability of nitrogen to bunchgrasses is more dependent on temporal environmental cues than spatial distribution, as these species have limited capacity to forage spatially for soil nutrients (Briske & Derner 1998). The dual demand-and-supply-led method employed in this model is proactive because it reduces resource wastage by downgrading growth during resource-poor periods and upgrading growth during resource-rich periods. It also ensures that some resources are always allocated to shoots, which is essential because individual leaves have a set life-expectancy so bunchgrass plants must continually grow new leaves in order to maintain photosynthetic machinery.

A further criticisim of the previous co-ordinated root-to-shoot partitioning models referred to in this chapter is that they are very simple differential equation models (Thornley & Johnson 1990; Reynolds & Chen 1996). As such they consider roots and shoots as two biomass pools that source environmental resources and compete for internal ramet groups. Due to this very simplified approach, these models ignore the feedback delays on resource supply introduced by the growth and death of individual organs and they ignore spatial resource availability effects. It is precisely because the feedback delay is ignored that these models produce such convincingly stable growth dynamics. Consider bunchgrasses growing in a closed sward. Allocation of most resources to roots during nitrogen-poor periods would reduce the size of leaves growing during that period. Photosynthesis would initially be maintained at sufficient levels by the existing leaves which have blade surface in the top portions of the canopy, but would subsequently decline when these leaves begin to senesce as the new reduced leaves would have much lower photosynthetic productivity. Consequently carbohydrate supply would be compromised by the lack of sufficient photosynthetic surface on the reduced leaves. If this delay effect was included in the

93

previous differential equation models their behaviour would be far less stable, emphasising the need for an additional feedback signal to dampen the delay effect. The structure of the TILLERTREE model considers growth of individual organs directly, which necessitated seeking an approach that would dampen the delay effect of organ growth on root-to-shoot allocation.

The dual demand-and-supply-led partitioning model presented here does not claim to be the final solution to the complex problem of root-to-shoot allocation, but it provides a basis for further research into modelling root-to-shoot allocation. A weakness of the approach adopted here is that it does not consider structural root growth explicitly, but rather treats it as an amorphous biomass that is maintained in some functional balance with shoot growth. This approach is appropriate for the objectives of this thesis, which focuses on growth abilities of clonal bunchgrasses in terms of their shoot structural architecture and how this is modified by resource allocation. However, for a more detailed investigation into root-to-shoot partitioning, rules for root growth need to be made more explicit. Spatial foraging of roots leads to quite rapid shifts in root distribution and dieback (Arredondo & Johnson 1999), so biomass turnover and resource demand may be more substantial than accounted for in the present model. Presumably root growth could be represented structurally in the TILLERTREE model using root segment objects like tiller that link consecutively together to form a root 'tree'. Careful attention woud need to be given to rules governing recruitment of side roots, and rules of allocation during resource competition between root structures. Such an extension would necessarily require a 3-dimensional version of the model since root foraging is explicitly a 3-dimensional process (Hutchings & de Kroon 1994). The problem of explicit structural root growth will be addressed in subsequent research. For the remainder of this thesis, the emphasis shifts to the consequences of shoot architecture for growth and resource capture in bunchgrasses and how this is modified by disproportionate resource allocation.

Chapter 7:

Structural Adaptations for Overcoming Light Limitation

Bunchgrasses growing in open grasslands impose light limitation on themselves by the manner in which they grow. They expand blades vertically from meristems held close to the soil surface. As the leaves grow and die the overlying canopy increases in density, reducing light penetration to the ground surface in accordance with Beers' Law. This reduces penetration of light to the ground surface substantially (Knapp *et al.* 1998). Consequently new blades photosynthesise poorly in closed swards until they expand through most of the overlying canopy, and only those portions of the blade that are close to the top of the canopy will produce large amounts of photosynthate (Schimel *et al.* 1991). In addition, in bunchgrasses, new blades are forced to grow through the sheaths of older phytomers, during which time they are probably capable of little or no photosynthesis.

Bunchgrasses growing in environments with distinct growing and non-growing seasons are subject to severe photosynthetic limitation at the start of each growing season if they are not defoliated. This is because their live blades die back over the non-growing season and no new blades are recruited as the conditions are not conducive for growth. At the start of the next growing season, the bunchgrass tillers contain little or no live photosynthetic material and must expand new blades firstly through overlying sheaths and then through the dead canopy in order to reach sufficient levels of light to generate carbohydrates for survival and growth. This new growth must be supported by existing carbohydrate resources within the grass plants and particular adaptations designed to overcome light limitation. This critical resource period is here termed the Spring Photosynthesis Bottleneck.

Grass plants store small amounts of carbohydrate at concentrations of at most 10% by live mass (Danckwerts 1984; Farrar & Williams 1991). In addition their capacity for storage is limited by the amount of live mass they contain, which is substantially reduced during the non-growing season. This restricts their ability to overcome periods of photosynthetic limitation if their existing blade surface is insufficient to supply maintenance and growth requirements, because the stored carbohydrate may be insufficient to supply enough carbohydrate for regrowth of even individual leaves. Therefore plants must possess

a number of additional traits that help them overcome light limitation. These may be physiological, such as the acclimation of the photosynthetic light response to low light conditions (Bjorkmann *et al.* 1972; Givnish 1988), or structural, which are designed to overcome light limitation by raising photosynthetic organs into the upper layers or even above the overlying canopy.

In this chapter, I focus on structural characteristics of individual grass tillers that help them overcome the Spring Photosynthesis Bottleneck. Clearly the manner in which grass plants allocate resources during regrowth through a closed dead sward will have some significance for their ability to overcome photosynthetic limitation. In Chapter 6, disproportionate resource allocation between roots and shoots was explored. This is one obvious means by which bunchgrass plants can improve temporal resource allocation under light-limiting conditions, by increasing the relative proportion of resources allocated to shoots in order to grow photosynthetic surfaces. There is strong evidence for the shifts in root-to-shoot ratios in response to shifts in the light environment (e.g. Cruz 1995). Critically the behaviour demonstrated that temporal resource allocation efficiency has a substantial effect on the ability of grass plants to overcome resource limitations. In other words directing resource allocation into shoots during the early spring period increased photosynthetic capacity for subsequent growth.

Four potential structural adaptations were identified from the literature that might help tillers overcome light limitations in closed swards. These were shoot organ etiolation, non-linear growth of blades, increased live root mass survival over winter, and survival of residual photosynthetic surface through winter. The aim of this chapter was to determine the relative importance of the four identified growth properties to the regrowth potential of grass tillers. The following question was asked: Are bunchgrasses able to overcome carbohydrate limitation during spring regrowth in non-defoliated swards through one or more of the identified structural growth properties?

The properties were assessed by observing their effect on the growth of single-tiller ramets simulated with the TILLERTREE model. The TILLERTREE model treats the vertical spatial dimensions of individual organs explicitly, so it is suitable for analysing this problem of vertical organ growth and light distribution. I begin by giving a description of each property and how it was incorporated into the TILLERTREE model.

1 PROPERTIES THAT MAY IMPROVE SPRING SHOOT GROWTH

1.1 Ogan etiolation (E)

Etiolation of shoot organs is a well-documented response to low light levels (Hutchings & de Kroon 1994), and forms part of a shade avoidance syndrome (Smith 1982) employed by bunchgrasses and other non-shade plants. The benefit of such a property is obvious: the further a tiller is able to extend its leaves upwards through a closed dead canopy, the better the quality of light it will be able to source for photosynthetic production (de Kroon & Knops 1990). In addition, the increased blade sizes may increase total potential photosynthetic production.

Etiolated growth is easily incorporated into the TILLERTREE model by increasing the maximum potential lengths of individual organs. For the simulations, etiolated values for blades, sheaths and internodes of reproductive phase growth of *Themeda triandra* are taken from tillers that had been collected off a non-defoliated treatment at Ukulinga (Appendix A1). All simulations that do not include etiolation, use maximum potential organ length values collected from a treatment defoliated at the start of spring regrowth (Appendix A1). These values are presented together in Table 4.1 of Chapter 4.

1.2 Non-linear mass growth of blades (B)

During blade growth, blade extension and blade mass growth have a sigmoidal relation (e.g. Rawson & Turner 1982, Granier & Tardieu 1999). This emphasises extension over mass growth during the early period, which allows the tiller to extend the blade to greater lengths at a smaller resource cost. Whether the benefit of non-linear blade growth has developed as a result of evolutionary pressure or is simply a consequence of the constraints of structural growth is unclear, but its value in improving temporal resource allocation efficiency is apparent.

Sigmoidal blade mass growth can be applied to individual blade growth by using a goal-gap type function that requires two $awllb_{i,t}$ estimates, the minimum mass per unit length relation, $minawllb_i$, and the maximum mass per unit length relation $maxawllb_i$. The goal-gap is defined by the mass difference between the potential blade mass, $\Psi wlb_{a,t}$, calculated with $maxawllb_i$, and actual blade mass, $wlb_{a,t}$. The rate at which this gap is

reduced is determined by the ratio of the blade potential length so far, $\Psi llb_{\alpha,t-1}$, over the maximum blade potential length, $\max\Psi llb_i$. The strength of curvature is determined by the exponent, eb_i.

$$\Delta wlb_{\alpha,t} = \min awllb_i * \Delta llb_{\alpha,t} + \left(llb_{\alpha,t} \max awllb_i - wlb_{\alpha,t-1}\right)\left(\frac{\Psi llb_{\alpha,t-1}}{\max \Psi llb_i}\right)^{eb_i} . \qquad 7.1$$

The value of $\max awllb_i$ equals the previous $awllb_i$, so the two variables that may be manipulated are $\min awllb_i$ and eb_i. As $\min awllb_i$ gets smaller and eb_i gets larger, the ability of a blade to penetrate the dead matter layer will increase because the summed resource cost of early blade expansion decreases. The value of $\min awllb_i$ is also a species characteristic, and field data suggested that the $\min awllb_i$ of *Themeda triandra* tillers was about 0.000052 g mm^{-1} (Appendix A1).

1.3 Greater proportional live root mass survival during winter (R)

Increasing the proportional root biomass during winter provides two benefits. Firstly, maintaining more live biomass through winter would allow bunchgrass plants to retain more carbohydrates in storage, thereby increasing their regrowth potential. Secondly the increased root-to-shoot ratio that would occur at the start of spring regrowth would reduce the demand placed by roots for growth. If the root-to-shoot ratio was sufficiently skewed the partitioning function would induce dieback of the root in order to restore the functional balance, which would supply additional carbohydrate and resources for re-allocation to shoot growth.

The idea that more live material survives the winter which increases the capacity for resource storage is a possibility. A number of studies have claimed that certain species, notably grasses and other species with low nitrogen contents, survive in low nitrogen environments partly because their roots survive for longer periods (e.g. Craine *et al.* 2002).

To simulate the effect of increased root mass survival through winter in the model, the root-to-shoot ratio is fixed at the $\max alrlsh$ during winter$_i$. This increases proportional live root mass surviving through winter, while shoot mass is determined by the mass of individual organs.

1.4 Survival of residual live photosynthetic surface through winter (L)

Survival of residual photosynthetic biomass into spring could provide two benefits to tufted grasses. Firstly the additional live biomass would provide additional capacity for carbohydrate storage. Far more importantly, maintenance of some live photosynthetic surface through winter would allow plants to begin photosynthesis immediately once growth resumes in spring.

There is a dearth of information on the survival of photosynthetic matter through the non-growing season. At Ukulinga, in the Southern Tall Grassveld, it was observed that most live tillers on bunchgrass species growing at Ukulinga maintained some live leaf material during the non-growing period (Figure 7.1). Other researchers have recorded this residual green biomass (e.g. Vasil'yev 1956). It has also been documented that certain plants' leaves 'green up' once water is added to the system (Van der Willigen *et al.* 2003; Vicre *et al.* 2003). From the lack of directed research into this topic, it remains unclear whether survival of green photosynthetic surface on grasses is the norm or a property only employed by certain species.

To simulate this effect the model is prevented from senescing the last two blades recruited in the first season further down than when they exceed the top of older overlying sheaths by 100 mm. This ensures that they are capable of some photosynthesis, though the efficiency might be reduced by the overlying dead LAI. Two blades are chosen because this is the number of live surviving blades found on *Themeda triandra* tillers at Ukulinga (Figure 7.1). These blades that have been kept alive through winter begin to senesce as soon as spring regrowth commences.

2 SIMULATIONS

Carbohydrate limitation arises because of seasonal shifts in photosynthetic productivity and limitation on carbohydrate storage. Photosynthesis is limited by light attenuation through the canopy (Chapter 3). The light environment is set by the shoot structure, which is defined by the seasonal growth behaviour of the considered species.

A reference simulation was conducted in which the growth of *Themeda triandra* was simulated without resource restriction and with none of the growth properties identified above applied in order to provide data for growth of the species under optimal conditions
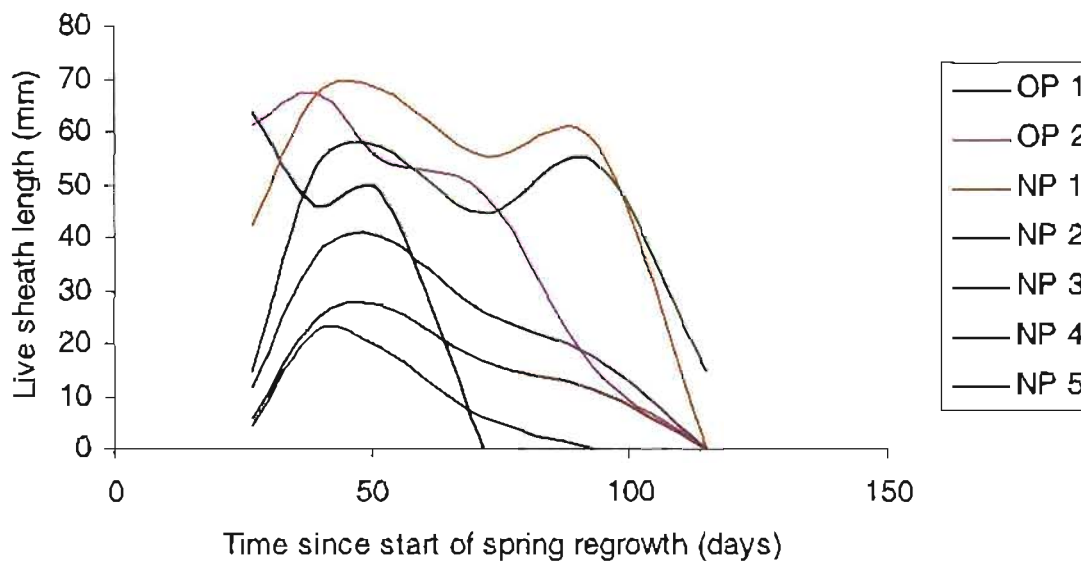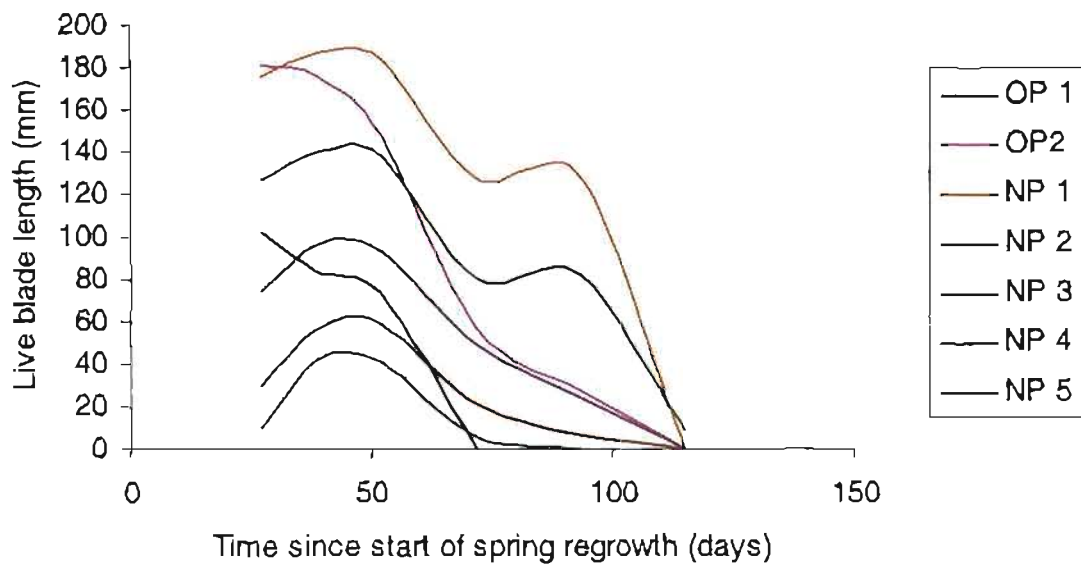
Figure 7.1 Live blade length and sheath length on consecutive phytomers that contain live leaf material. Data collected at Ukulinga during the 1999/2000 growing season (see Appendix A1 for details). (OP – phytomers recruited and expanded prior to the start of spring regrowth, NP – phytomers expanded subsequent to the start of spring regrowth).

and also to identify periods in which carbohydrate demand exceeds supply from photosynthesis. A second simulation of this nature was conducted with etiolated organ lengths because this adaptation changes the size of the tiller.

Following this, a 2^4-factorial experiment was conducted in which the growth of *Themeda triandra* tillers was simulated for all treatment combinations of the four properties, with restriction on maximum carbohydrate retention in the AVC set at 15% of live mass. This included a control with none of the properties applied. Performance was measured by ability to survive in spring through to the completion of flowering and by the magnitude of the spring growth response measured in terms of maximum live blade mass, sheath mass and root mass achieved during the second season of growth.

2.1 Model assumptions

a. The environment was separated into two periods, a growing season and a non-growing season. Plant activity (photosynthesis, growth, maintenance, senescence) was set at maximum rates during the growing season. During the non-growing season, growth and photosynthesis were inhibited and maintenance was reduced to 0.1 of its growing season value in order for turnover processes to proceed. Blade dieback proceeded during winter on all live blades except the youngest blade, which survived the winter period intact. This assumption was based on the observation that *Themeda triandra* tillers in the Southern Tall Grassveld maintain at least one live blade during winter (personal observation).

b. Allocation between roots and shoots is controlled by the dual demand-and-supply partitioning model described in the previous chapter.

c. Nitrogen is not limiting to growth. Our interest is only in the availability and allocation of carbohydrate even though the root-to-shoot partitioning function considers the availability of both carbohydrate and nitrogen. There is evidence both from the simulations in the previous chapter and from empirical research to suggest that early regrowth is not limited by nitrogen (Bausenwein, Millard & Raven 2001, Lamaze, Pasche & Pornon 2003).

d. Light penetration through a canopy is a property of individual species that relates to organ angles to the ground and transmission properties of those organs, summarised in the

light extinction parameter K. This model uses a value for K of 0.67 for an upright bunchgrass (Humphreys 1991). The size of LAI is adjusted by the ground surface area (GSA) over which the LAI is calculated (see Equation 3.8, Chapter 3). The LAI estimate uses a GSA = 20.0 cm^2, which gives an LAI generated by the single-tiller ramet at the start of spring of 3.07 m m^{-1}, which is similar to empirical estimates for a non-defoliated sward at Ukulinga (see Appendix A1).

3   RESULTS

3.1   Reference simulation - growth with no carbohydrate restriction

When resources are non-limiting, the model will allocate resources between roots and shoots at the midalrlsh$_i$ value and imbalance will be constant at zero for the duration of the simulation. This is shown by the fixed ratio of live root-to-shoot mass (Figure 7.2). The temporal growth distributions of different organ types throughout the lifecycle of the grass plant are also illustrated (Figure 7.3).

The resource supplies and demands indicate that photosynthetic production during the first season is sufficient to meet the growth requirements of the single-tiller ramet (Figure 7.4). This is because the plant always has some live blade surface exposed to direct sunlight which is therefore capable of maximum photosynthetic rate, and also because daily demands are small relative to supply rates. However during the second season there are periods when growth demand exceeds photosynthate production. Notably in both simulations, carbohydrate demand for regrowth is relatively large during the spring regrowth phase and early regrowth at this time is entirely dependent on re-allocation of internal carbohydrate resources to supply this demand. Grass plants are able in part to overcome this deficit by temporal separation between blade growth and stem elevation and floral growth during the second spring (Figure 7.3). This allows the plant to accumulate photosynthetic surface to provide resources for the resource-demanding reproductive stage and reduces the absolute daily demand.

There are a number of periods of sharp carbohydrate release from storage. These are associated with periods when the ratio of net photosynthate after maintenance has been supplied (CNetPs$_{Y,t}$ − Cmaint$_{Y,t}$) to growth demand (Cgrow$_{Y,t}$) falls below 1. The largest decrease in photosynthesis occurs once photosynthesis halts after reproduction is completed,
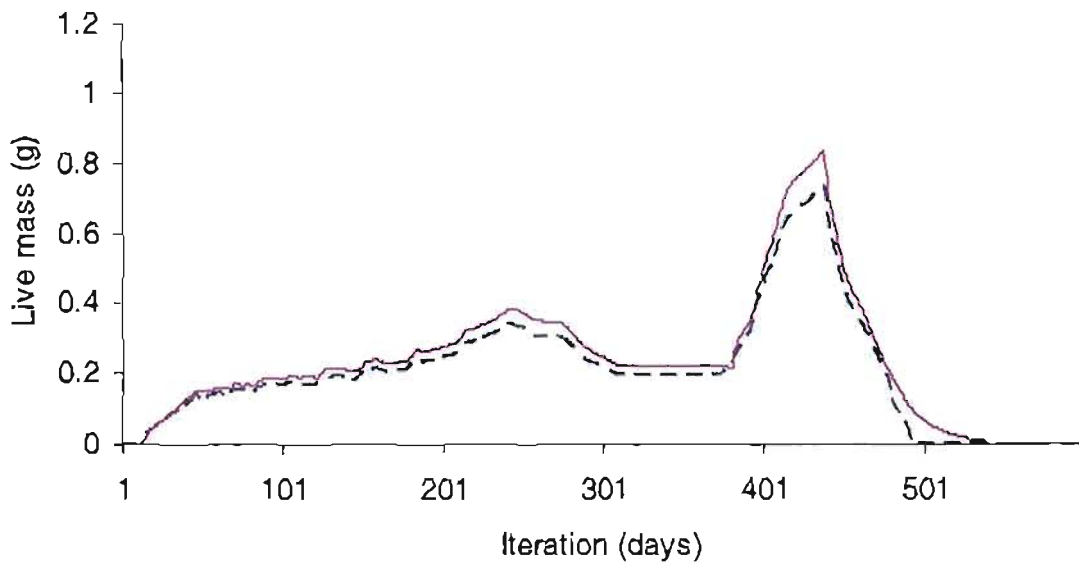
Figure 7.2   Change in live root mass (————) and live shoot mass (— — —) of a single-tiller ramet that has no resource limitation. Root-to-shoot allocation responds to the resource imbalance function. (Environmental conditions: Plant activity during the growing and non-growing season as defined in Section 4.3 of Chapter 4. Growing season proceeds from Yearday 1 to Yearday 242 of each year. Soil nitrogen is not limiting to growth.)
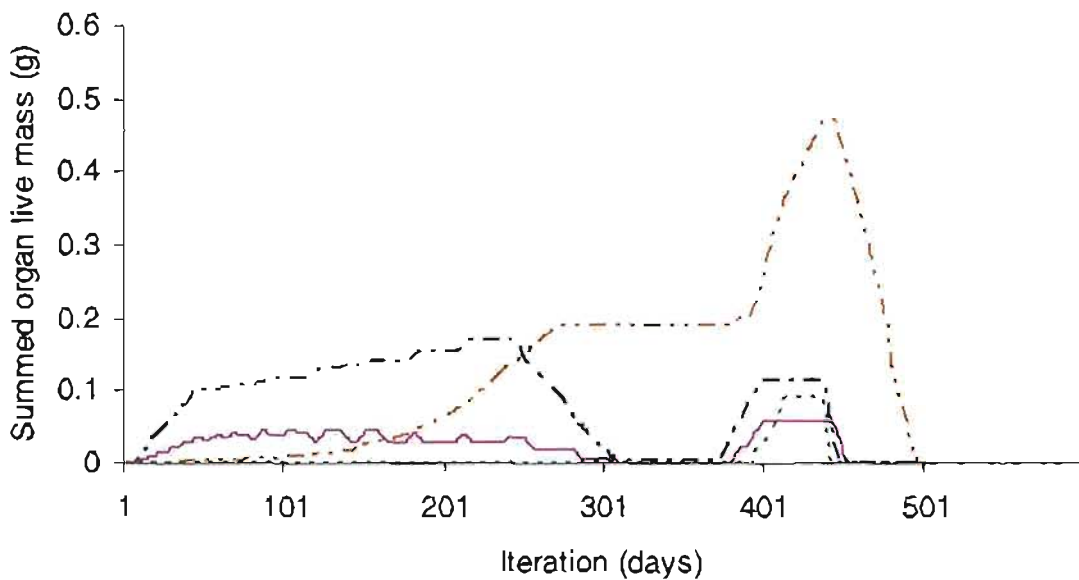
Figure 7.3   Summed live mass of organ types (— · — blade mass; ———— sheath mass; — · — internode mass; — — — flower mass) of a single-tiller ramet that has no resource limitation. Root-to-shoot allocation responds to the resource imbalance function.   (Environmental conditions: Plant activity during the growing and non-growing season as defined in Section 4.3 of Chapter 4. Growing season proceeds from Yearday 1 to Yearday 242 of each year. Soil nitrogen is not limiting to growth.)
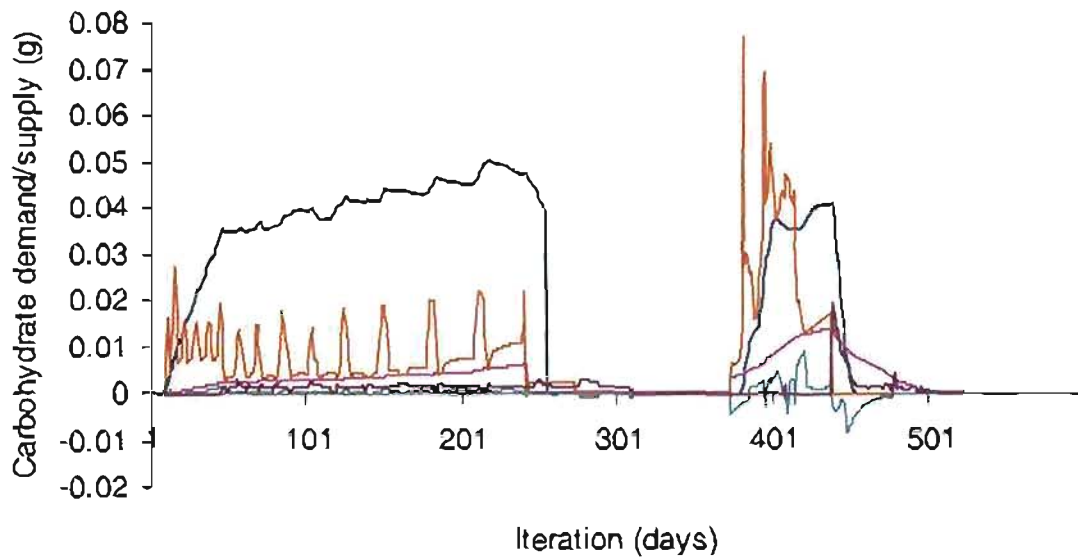
Figure 7.4 Daily carbohydrate demand and supply of a single-tiller ramet that has no resource limitation. Root-to-shoot allocation responds to the resource imbalance function. No defoliation is applied. (———— Net photosynthesis supply; ———— maintenance demand; ———— growth demand; ———— storage demand; ———— dieback supply.) (Environmental conditions: Plant activity during the growing and non-growing season as defined in Section 4.3 of Chapter 4. Growing season proceeds from Yearday 1 to Yearday 242 of each year. Soil nitrogen is not limiting to growth.)

which may be ignored in the context of the problem. Other periods of storage release occur at the start of spring regrowth indicating photosynthetic limitation, and during the early phase of stem elevation indicating a large growth demand of simultaneous internode expansion on multiple phytomers.

3.2   Effect of growth properties under carbohydrate restriction

The data generated by the 4-factorial design of treatment combinations is presented in Table 7.1. Three treatments were unable to overcome photosynthetic limitation during early spring, namely the control simulation, the simulation with only the etiolation property added to growth and the simulation with only the non-linear blade mass growth added to growth. All other simulations survived through to the completion of floral growth and natural senescence but with different levels of success, as demonstrated by the maximum live masses achieved. This included the two simulations with only increased proportional winter root live mass and surviving live photosynthetic surface respectively, but growth in both of these simulations was extremely poor, indicating that the plants were severely limited by photosynthetic production.

Simulations in which two of the properties were included improved growth substantially, except for the combination of non-linear blade mass growth and increased proportional winter root live mass. This indicates that etiolation and surviving live photosynthetic surface each provided a greater benefit in combination with other properties, and together provided sufficient benefit to completely overcome resource restriction. All other 2-property strategies experienced substantial growth restriction caused by carbohydrate limitation, indicated both by poor growth and greater shoot growth than root growth.

Table 7.1   Maximum live masses achieved in the second spring by simulated single-tiller ramets in a 4-factorial experiment with etiolation (E), non-linear blade mass growth (B), greater proportional winter root mass (R), and surviving residual live photosynthetic surface (L)

Treatment	Variable		
	Blade mass (g)	Shoot mass (g)	Root mass (g)
Non-restricted values	0.115	0.659	0.756
	(E: 0.199)*	(E: 0.881)	(E: 1.003)
Control	0.007	0	0
E	0.009	0	0
B	0.007	0	0
R	0.025	0.150	0.075
L	0.045	0.243	0.124
E+B	0.098	0.700	0.564
E+R	0.058	0.289	0.123
B+R	0.021	0.160	0.074
L+E	0.184	0.848	0.966
L+B	0.040	0.269	0.155
L+R	0.055	0.301	0.168
E+B+R	0.152	0.791	0.900
L+E+B	0.162	0.828	0.943
L+E+R	0.188	0.891	0.988
L+B+R	0.058	0.406	0.274
L+E+B+R	0.165	0.857	0.950

• maximum live mass achieved with etiolation

Simulations that combined three properties included were all capable of substantial growth in spring, except the treatment without etiolation (L+B+R), indicating that etiolation played the most substantial role in spring regrowth, but that it required at least one of the other properties to increase the temporal growth efficiency during early spring regrowth. The simulation in which surviving live photosynthetic surface was excluded (E+B+R), also grew substantially. This indicates that single-tiller ramets were able to overcome carbohydrate limitation in spring with the combination of the three growth properties in the absence of surviving live photosynthetic surface. However it is important to note that this E+B+R combined strategy was subject to carbohydrate limitation throughout the period of blade expansion in the second spring (Figure 7.5).

Only the E+B+R+L combined strategy was not restricted by carbohydrate limitation during this period (Figure 7.5). Therefore it is clear that maintaining some photosynthetic surface through winter has a strong positive effect on net carbohydrate balance.

4   DISCUSSION

The combined evidence indicates that bunchgrass ramets with little or no live photosynthetic material can regrow new photosynthetic surface sufficiently to overcome light limitation in closed swards, even though their potential to store carbohydrate reserves is fairly restricted. They do this through a series of complementary structural properties.

The simulations demonstrated that tillers could overcome resource depletion without surviving residual photosynthetic surface, and that the most important property was etiolation, confirming a large body of empirical evidence linking this property to light foraging (Hutchings & de Kroon 1994). However, etiolation on its own was not sufficient to overcome the resource limits. Combining sigmoidal blade mass growth with etiolation was an effective strategy because the non-linear increase in blade mass with extension improved temporal resource-use efficiency by allowing the tiller to reach higher into the canopy for a lower nutrient cost. These properties combined with disproportionate resource allocation between roots and shoots allowed single-tiller ramets to overcome light restriction sufficiently to avoid death, indicating that temporal resource-use efficiency is a probable strategy employed by bunchgrasses to avoid death in moribund swards. Leaf etiolation and non-linear blade mass growth combined with disproportionate allocation between roots and shoots were, however, not sufficient to overcome light limitation during the second growing
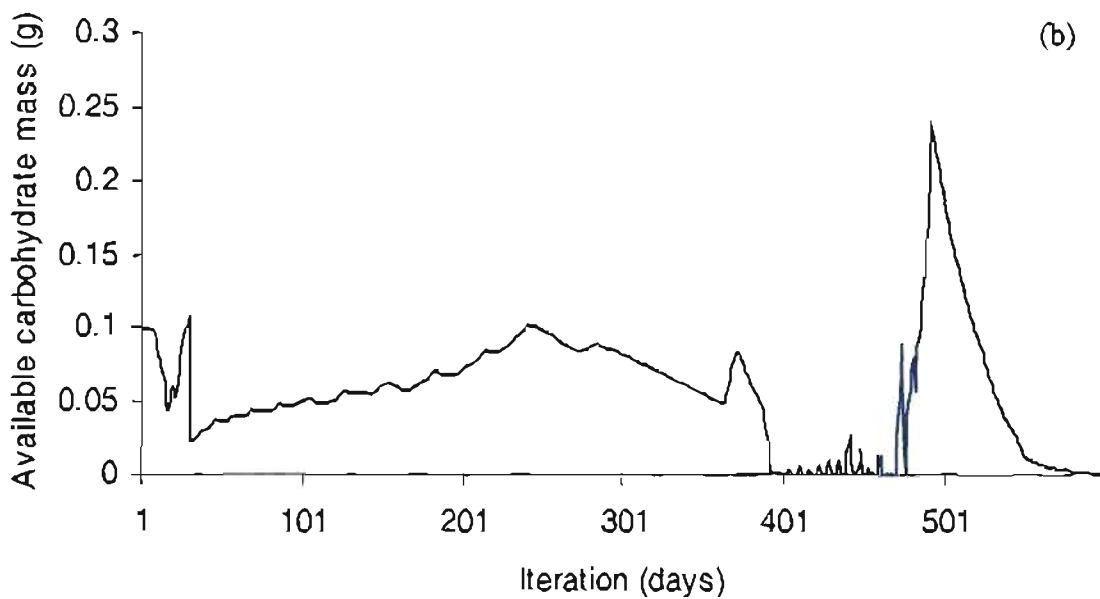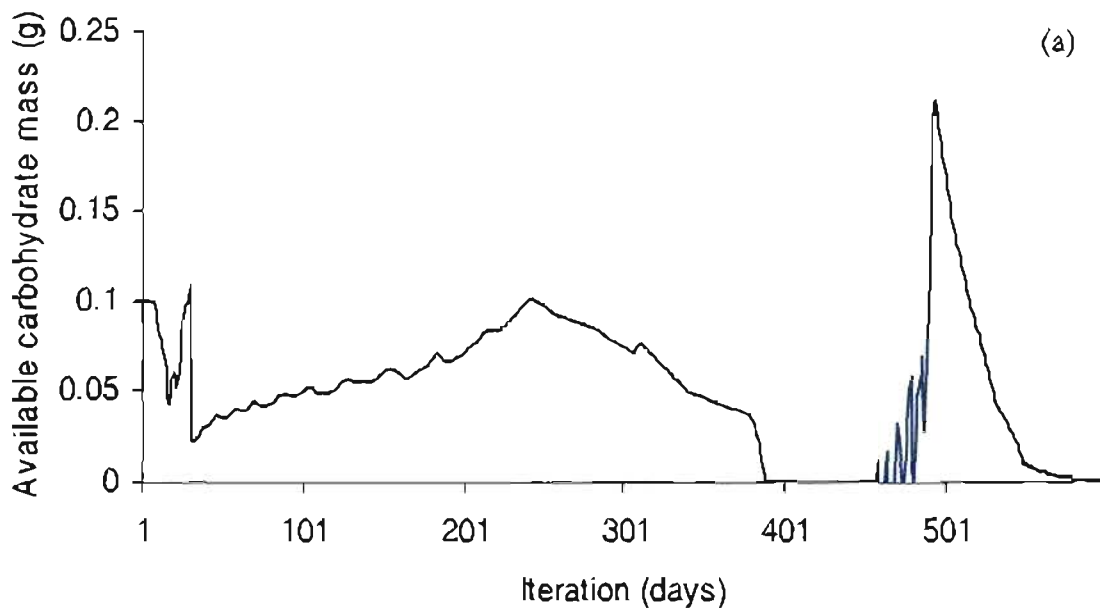
Figure 7.5 Comparison of carbohydrate retained in the AVC at the end of each iteration for the simulated single-tiller ramet that did not maintain live photosynthetic surface through winter, E+B+R (a), and that which did retain live photosynthetic material through winter, E+B+R+L (b). (Environmental conditions: Plant activity during the growing and non-growing season as defined in Section 4.3 of Chapter 4. Growing season proceeds from Yearday 1 to Yearday 242 of each year. Soil nitrogen is not limiting to growth.)

season, and consequently growth was still substantially reduced in the absence of the other considered structural adaptations.

The importance of sigmoidal blade mass growth to temporal resource-use efficiency during light foraging does not appear to have been considered previously. There is evidence that etiolated blades have a lower mass-to-area ratio than non-etiolated blades (Givnish 1988; Mojzes, Kalapos & Virágh 2003), suggesting that etiolation does itself lead to greater resource-use efficiency through changes in leaf allometry. This property was ignored for the present study because there is no clear data on how etiolation affects the mass-to length ratio of bunchgrass leaves, nor any corroborative data on whether comparable leaves grown in sun and shade have the same net mass, in which case changes in leaf allometry would certainly increase resource efficiency. To the contrary, there is evidence of increased allocation to leaves relative to other shoot organs under shaded conditions (e.g. Rice & Bazzaz 1989), which suggests that leaves on shaded plants are heavier than light-grown plants. Given the length and upright growth of leaves of bunchgrasses, it is improbable that bunchgrasses could afford the loss of tensile strength in individual leaves growing through closed swards that would result from a change in the mass-to-length ratio. This suggests that sigmoidal blade mass growth, although only a temporal effect, provides a real benefit to bunchgrass tillers growing through closed canopies.

The temporal resource efficiency demonstrated here arises from the combined effects of structural adaptations and disproportionate resource allocation. The combined effects were demonstrable because the TILLERTREE model considers both bunchgrass architecture (phytomer object arrangement and growth) and resource allocation explicitly. Most previous models have been unable to consider these interactions because either they concentrated on disproportionate resource allocation and did not consider structure sufficiently explicitly (e.g. Reynolds & Chen 1996; Herben & Suzuki 2002), or they considered structure explicitly and avoided resource allocation (e.g. Prusinkiewicz & Lindenmayer 1990).

The combined evidence indicates that *Themeda triandra* plants are carbohydrate-limited during spring regrowth even if they maintain some live photosynthetic material over the non-growing period, and only the simulation which included all four structural adaptations (etiolation, non-linear blade mass growth, increased root mass survival, and survival of residual live photosynthetic surface) overcame carbohydrate limitation during spring regrowth (Figure 7.5). That said, survival of live photosynthetic material over winter did improve the growth response. These results have significance for the seasonal growth of

bunchgrasses, as they suggest that seasonal growth in non-defoliated bunchgrass swards will depend strongly on the amount of live photosynthetic surface maintained over the previous non-growing season. If the amount is small, then carbohydrate limitation will be severe and initial regrowth will be slow, while if it is large then carbohydrate limitation will be less restrictive and initial regrowth will be more rapid. This in turn will affect the bunchgrass swards' ability to capture soil nitrogen, which is greatest at the beginning of the growing season in humid grassland communities (Blair *et al.* 1998), which will affect the subsequent growth potential of the bunchgrasses, as nitrogen is the most limiting nutrient to growth. Environmental conditions that might cause substantial desiccation of live photosynthetic surface include frost and severe drought (Walters *et al.* 2002). In environments subjected to varying degrees of winter frost, such as the Southern Tall Grassveld (Acocks 1953), this means that growth in non-defoliated swards in any given growing season could be dependent on the severity of frost in the previous winter, which would determine the amount of surviving residual biomass. Thus seasonal productivity is temporally dependent on events that occur prior to the season and productivity cannot be estimated from within-season rainfall alone.

The simulations indicate that there would certainly be a benefit from increased root survival through winter because additional carbohydrate can be assigned to shoot growth in spring both from storage and root dieback, even if the concept of root dieback during spring seems unlikely as a growth strategy. One trade-off of such a strategy would be the reduction in nitrogen absorbed while resources are allocated to shoot growth. This might prove too expensive in a humid grassland community where nitrogen is very restrictive to potential growth across the entire season (Knapp *et al.* 1998) even if it is non-limiting during spring (Bausenwein *et al.* 2001, Lamaze *et al.* 2003). It may be that root dieback occurs on some structures while other roots start to grow during spring. The model is unable to assess this effect presently because it treats roots as an amorphous mass.

The benefit given by greater root survival through winter indicates that increased biomass survival over winter increases the subsequent spring growth of bunchgrasses because more resources are available for early spring regrowth, which increases the ability to capture soil nitrogen in spring and therefore promotes seasonal growth. This provides a probable explanation for the noted positive relationship between biomass production in a given year and biomass production in the next year (O'Connor, Haines & Snyman 2001): greater biomass accumulation in the present year will increase biomass survival over the

subsequent winter, thereby increasing resource availability for growth in the subsequent growing season.

The simulations indicate that bunchgrasses overcome light limitation at the start of spring through maximum allocation to the first emerging blade. This indicates that properties of phytomer growth in early spring and phytomer survival through winter are critical to the behaviour. These properties are understudied. Of interest here is the growth and dieback of leaf blades during unfavourable growth periods. Critically, assuming that dormancy in C_4 grasses is imposed by environmental conditions, what are the effects of unfavourable growth periods on phytomer development? Do these periods induce growth phase change (e.g. induction of the plateau phase)? Do unexpanded phytomer numbers accumulate during these periods? The latter would cause simultaneous growth of multiple blades when conditions for growth become favourable once again, which might place additional stress on regrowth during spring.

The present chapter considers the growth of a single-tiller ramet only. Once secondary tiller recruitment is incorporated, the demand for resources will increase and the increased growth will further reduce photosynthetic efficiency as the LAI increases. This effect is described in Chapter 8, and it is demonstrated that multi-tiller growth further compromises the total growth of individual reproductive tillers.

SECTION 3

Multiple Tiller Dynamics and Growth of Single Clones

In this section, recruitment of secondary tillers is enabled, which allows the formation of multiple tillers on ramets, multiple ramets formed when daughter tillers root, and multiple ramet groups formed when vascular connections among familial ramets are broken. This allows us to observe how bunchgrass clones grow. In the simulations conducted here, an individual clone starts growth through the intiation of a single ramet with a single tiller, which then grows and recruits daughter tillers and ramets within the resource limits of the defined environment.

In Section 2 structural growth and resource allocation between shoots and roots in bunchgrass plants were observed in the simplest manner using single-tiller ramets. It was demonstrated that the productivity of bunchgrasses shows strong temporal dependence that relates to their ability to capture the single resource light, which results from the structural manner in which they grow and the seasonal nature of the environment they inhabit. The single ramet simulations ignored the effects of nitrogen availability on growth behaviour.

In this section, nitrogen limitation is included in the modelled environment. Nitrogen is the most limiting mineral nutrient in grassland environments. Therefore the ability of grass plants to capture and utilise this resource is of critical interest, as this bounds their growth potential.

The section is divided into two chapters. Chapter 8 examines the interactions between the architectural arrangement of objects on bunchgrass clone (tillers, ramets, ramet groups) and proportionate versus disproportionate resource allocation between objects, on the growth of individual bunchgrass clones. Included in this chapter is an assessment of why bunchgrass plants disintegrate and what resources are likely to control tiller recruitment.

Chapter 9 uses the information derived in Chapter 8 to assess the effects of changes in the organ properties, leaf length and daily growth rate, on the ability of bunchgrass clones to grow and capture nitrogen. These organ properties are associated with the distribution of bunchgrass species, and the behaviour recorded in Chapter 9 provides evidence for a trade-off in competitive ability that is associated with these properties that results from the relationship between architecture and resource allocation of bunchgrass clones.

Chapter 8:

Interactions between Population Dynamics and Resource Allocation

Indvidual bunchgrass clones are composed of multiple tillers, ramets and ramet groups. These together form the population architecture of individual bunchgrass clones that arises from the manner in which bunchgrasses grow (Briske & Derner 1998). There is competition for resources at a number of levels. Within individual ramets and individual ramet groups there is competition between tillers and ramets respectively for available internal resources. At the clonal level, there is direct competition between disconnected ramet groups to acquire and utilise available environmental resources (Tuomi & Vuorisalo 1989). Clearly the relationships are complex, so disproportionate resource allocation between physiologically connected objects at lower levels (tillers, ramets) could determine behaviour at higher levels (ramets, ramet groups, clonal performance).

Two critical components of resource allocation are tiller recruitment, and disproportionate resource allocation among existing live objects. The ability to recruit tillers rapidly and kill tillers disproportionately may allow bunchgrasses to respond appropriately to the variability of the environment they inhabit. Growth and death of tillers leads to rapid, although not necessarily discontinuous, changes in resource demand and supply of individual rooted plants and ramet groups. It has been proposed that tiller recruitment in bunchgrasses is mediated by signals that reflect the availability of environmental resources, light and soil nitrogen, which ensure that they grow appropriately in response to resource availability (Tomlinson & O'Connor 2004). Disproportionate allocation of resources between connected objects provides a means by which plants can improve resource-use efficiency by promoting growth of more productive structures and downgrading growth of less efficient structures (Bangerth 1989; Sachs *et al.* 1993).

A third component that may contribute to the competitiveness of bunchgrass clones is non-integration of individual clones (Kelly 1995) into smaller, competing units (ramet groups), which may improve the resource allocation efficiency across the clone. Together these three components form part of an integrated growth strategy, by which is meant that clonal behaviour generated by one component is dependent on the other components.

In this chapter, each of the three components is assessed to see how they affect the productivity of bunchgrasses in response to limitation by two resources, light and soil nitrogen. Before proceeding to assess each of the three components, the rules for tiller recruitment are introduced as these are necessary to simulate multiple tiller growth in the TILLERTREE model.

Resource allocation between connected live structures is addressed first. Rules for disproportionate allocation are introduced and the behaviour of clones is simulated under proportionate and disproportionate resource allocation. Subsequently clonal integration is tested and interpreted in the light of the results obtained from the resource allocation simulations. Lastly, the resource requirement rules for tiller recruitment are revisited in the light of proportionate and disproportionate resource allocation in order to determine their effect on the clonal growth.

1   TILLER RECRUITMENT

The rules that govern tiller recruitment are not well understood, and the underlying mechanism that controls tiller recruitment has not been elucidated. As part of this project an extensive review of the published research was conducted that identified the main variables affecting tiller recruitment. This information was then united into an integrated model of plant control over tiller recruitment. This review is presented in Appendix A2. In this section only the major findings of this effort shall be discussed in order to formulate rules for the model.

Tiller recruitment in clonal plants is a subset of the problem of lateral bud outgrowth in higher plants. Three supposedly competing hypotheses of lateral bud outgrowth have been proposed, namely apical dominance, the nutrition hypothesis and photosensitivity to the red: far-red light ratio. The apical dominance hypothesis proposes that tiller recruitment is inhibited by apical control in existing growing tillers (Cline 1991). The nutrition hypothesis proposes that tiller recruitment is controlled by resource availability (Gregory & Veale 1957). When resources required for tiller recruitment exceed the demands placed by existing structures in a plant these resources may be allocated to secondary tillers, and hence lateral bud outgrowth is stimulated. The R:FR hypothesis proposes that tiller recruitment is mediated by plant phytochrome responses to shifts in the R:FR light ratio (Derigibus, Trlica & Jameson 1982). Thus control over tiller recruitment forms part of the shade avoidance

syndrome. Greater tiller recruitment in response to reductions in existing tiller density (Butler & Briske 1988) may reflect this process.

The three supposedly competing hypotheses may be linked in a logical fashion. In addition there is strong evidence to suggest that the balance among the three processes is both a function of the environment and plant form. The integrated model maintains the accepted paradigm that actual bud release is hormonally controlled by the auxin:cytokinin ratio, which reflects the availability of carbohydrate and nitrogen resources. Local resource concentrations may also be inhibitory. Importantly, each hormone is controlled by local signals in the shoots and roots respectively facilitating appropriate responses to environmental conditions. Auxin production and export from the shoots is moderated by phytochrome responses to red: far-red light ratios. Further, the phytochrome equilibrium (Pfr/P) manipulates organ size and hence resource supply. By this means the Pfr/P may affect instantaneous growth demands by manipulating organ size in response to R:FR light shifts. Under low R conditions this would direct more resources towards lateral buds and away from inactive lateral buds.

Cytokinin production is mediated by root nitrogen concentration, which in turn is a function of nitrogen absorption from the soil and seasonal re-allocation of tissue nitrogen. An examination of the growth form of bunchgrasses and the environment in which they are found emphasise that nitrogen has a strong mediatory role over tiller production which allows the grass plant to respond appropriately to shifts in this limiting resource. Notably seasonal patterns of tiller recruitment (e.g. Tainton & Booysen 1965) are associated with periods of high soil nitrogen availability to plants (Birch 1958). This suggests that control of lateral bud outgrowth may have an evolutionary basis in resource competition.

Traditionally apical dominance was considered to inhibit tillering, but Briske & Silvertown (1993) cite numerous references showing that the results are inconsistent with this hypothesis. Tiller recruitment does occur on plants with intact meristems (e.g. Tainton and Booysen 1965; Danckwerts 1984; Murphy & Briske 1992) and intensive grazing may decrease the tillering response of tillers relative to less intensively and even non-grazed tillers (Olson & Richards 1988b). It would seem that the primary purpose of apical dominance is to direct growth resources preferentially to the most photosynthetically-active tillers (Bangerth 1989; Bangerth et al. 2000).

The model does not consider auxin or cytokinin explicitly. The above arguments suggest that these hormones probably act as cues that reflect the availability of carbohydrate and nitrogen for growth to ensure that the plant expends resources on secondary tiller

112

recruitment at appropriate times. Therefore the model uses the internal concentrations of AVC and AVN to direct tiller recruitment, on the assumption that auxin and cytokinin concentrations are directly related to internal carbohydrate and nitrogen concentration. An additional benefit of using AVC and AVN is that stored carbohydrate and nitrogen do not affect tiller recruitment directly as the carbohydrate and nitrogen bound in stored components does not affect resource concentrations. The position taken in this model is that as long as the apex is intact, the primary focus of the grass plant is to allocate resources to existing structures first. New daughter tillers are created when there are excess non-structural reserves of carbohydrate and nitrogen. This satisfies the observed tillering response of grasses that have been defoliated or even apically decapitated. If the defoliation regime is intense, then the reserves are low and the tiller cannot produce secondary tillers. Consistent defoliation is likely to reduce tiller recruitment while intermittent defoliation may increase tiller recruitment at each recruitment event (Briske & Silvertown 1993). If, on the other hand, defoliation removes the stem apex, the tiller's own growth is terminated. It will then focus all resources into secondary tiller recruitment. The degree to which it recruits tillers will depend on the amount of stored reserves and remaining leaf surface able to provide carbohydrate for tiller recruitment. Tiller recruitment on *Themeda triandra* is significantly enhanced by spring burning (Tainton & Booysen 1965) because resource storage is high during this period and the apical meristems of existing tillers are often destroyed by fire. Low levels of tiller recruitment were recorded for the species after defoliation during the middle of summer (Tainton & Booysen 1965), presumably because resource reserves are small at this time.

Tiller recruitment rules are divided into those that regulate tiller recruitment events and those that define where new tillers get recruited during a tiller recruitment event.

1.1   Model rules for tiller recruitment

1. Tiller recruitment can only occur on phytomers up to and including the third youngest phytomer. This follows evidence from rice plants collected by Katayama (1951) (cited by Nemoto *et al.* 1995) that an axial bud may only differentiate three phyllochrons after the phytomer with which it is associated has been recruited. This means that tillers with less than three expanded phytomers are unable to recruit secondary tillers.

2. Each live tiller may only recruit one secondary tiller in a single day iteration.

3. A live tiller may only recruit secondary tillers if it has passed a minimum mass $(wl\beta_{\beta,t} > 0.01$ g) in order to prevent poorly-growing tillers from recruiting secondary tillers.

4. It is assumed that there is an interval (in days) between consecutive tiller recruitment events on each primary tiller. This rule controls how many tillers are recruited during favourable environmental conditions. Sensitivity analysis indicated that values ranging from 3 to 12 days produced reasonable model behaviour. Below this range model behaviour was unstable because of the overproduction of tillers and beyond this range the recruitment interval hindered tiller recruitment and therefore the ability of the clone to utilise temporally-available resources. The coefficient of variation for annual nitrogen accumulation across the 10 simulations with intervals ranging from 3 to 12 days was 6.7%. For the simulations that follow the recruitment interval was set at seven days.

5. Secondary tiller recruitment may occur on any day if, after maintenance, storage and growth of existing plant structures have been satisfied, there are sufficient excess resources available for allocation to secondary tillers. Therefore both AVC and AVN must exceed some minimum concentration.

$$
Tillering = \begin{cases} 1 & if \quad \left(\dfrac{AVC_{\gamma,t}}{wl\gamma_{\gamma,t}} \geq 0.02\right) AND \left(\dfrac{AVN_{\gamma,t}}{wl\gamma_{\gamma,t}} \geq 0.01\right) \\[2em] 0 & otherwise. \end{cases} \qquad 8.1
$$

The values used were chosen on the basis of order of magnitude only. Doubling these values both separately and simultaneously across different recruitment intervals led to a maximum absolute change in annual nitrogen accumulation of 13.4% and a mean absolute change of 7.8%.

6. Tiller recruitment is inhibited if environmental conditions are unsuitable for growth as discussed in Chapter 4. Therefore if soil water potential is too low for growth (< -1500 Pa) or minimum temperature too low for growth (< 8 °C) during the possible winter months (May to September), recruitment is inhibited.

1.2 Model rules for placing recruited tillers

1. One tiller may be recruited at each axial node on each phytomer.

2. Tiller recruitment in bunchgrasses may occur near the apex of each tiller (Busso, Mueller & Richards 1989; Gibbs-Russell *et al.* 1990; Appendix A1), but it is clear that some species are only capable of tiller recruitment at basal internodes (Gibbs-Russell *et al.* 1990; Appendix A1). When a new tiller is recruited a search function is used to find an unoccupied node. The manner in which this search proceeds is user-defined. A search may start at the oldest phytomer and proceed forwards until it finds an unoccupied node. Alternatively, the search may be start at the third youngest phytomer and proceed backwards down the phytomer, if the species is able to recruit tillers on expanded culms. *Themeda triandra* does exhibit tiller recruitment on expanded culms, but the behaviour of culm tillers is not well-understood and their longevity has not been researched. Certainly it seems apparent that they rarely survive through winter (personal observation). Therefore because the behaviour of culm tillers is unclear, only basal tiller recruitment is allowed for the simulations in this thesis (secondary tillers are recruited from the oldest node outwards) in order to simplify the population behaviour by ensuring that all tillers have the potential to develop roots and form independent ramets. This ensures that the modelled *Themeda triandra* remains a simple representative for the bunchgrass growth form.

3. Occupied phytomer nodes may become available again for tiller recruitment, either if the secondary tiller at the node point dies or if the secondary tiller forms roots and splits off to form its own ramet.

4. Tiller type is determined by the nodal position at which the new secondary tiller is recruited. If the phytomer forms parts of the expanded culm, then the tiller is marked as a culm tiller. If the tiller is recruited on a basal phytomer in the non-expanded region on the stem of the parent tiller, then it is basal.

1.3 Rooting

Rooting on tillers is a critical consideration in the growth strategy of bunchgrasses as it directly determines the number of new ramets that are formed, and therefore has direct bearing on the demography of bunchgrasses. In reality it is probable that root formation is partly driven by environmental cues, but these are ignored here. Instead I use a very simple rule here in order to avoid the complexity that might arise from a variable rooting response.

Rooting on basal tillers is prevented before the tiller passes a certain minimum age on the assumption that it is limited by development criteria similar to tiller recruitment. Rooting only occurs on tillers recruited below a critical height on the assumption that rooting is ineffective if the tiller is raised too far above the ground surface.

$$root\ development\ =\ \begin{cases} 1 & if\ \ (Age\ \geq\ 30\ days) \cap (Basal\ height\ <\ 30\ mm) \\ \\ 0 & otherwise. \end{cases} \qquad 8.2$$

2 MODEL ASSUMPTIONS FOR MULTIPLE TILLER MODEL

2.1 Seasonal growth

In order to avoid unstable behaviour arising from spring regrowth through dead canopies, it is assumed for the simulations that follow that each plant is able to keep two leaves alive through winter. In addition maximum growth rates are possible during the growing season, while no growth can occur during the non-growing season. This ensures that behavioural differences arise strictly from differences in growth strategy and not additionally due to differences in growth response to environmental factors. These effects will be assessed subsequently to determine whether or not there are any differences in behaviour arising from this additional complexity.

In each simulation a single clone is initialised, which starts the growth of a single ramet with a single tiller. The model clone grows subject to the constraints placed by soil nitrogen availability (defined below) and the plant's ability to obtain light for photosynthetic production. The ground surface area (GSA) is set at 100 cm², which bounds the space available for photosynthesis and nitrogen absorption from the soil. The resource

values for carbohydrate and nitrogen used to start the clone are StartAVC = 0.1 g and StartAVN = 0.03 g respectively. The value of StartAVN ensures that the ramet can grow rapidly and occupy the given space. Each simulation is run for 10 000 iterations in order to determine if the model survives and stabilises, and subsequently to generate average data for the site across the simulated years.

2.2 Environmental nitrogen availability

It has often been stated that nitrogen is the most limiting resource to plant growth in tall grasslands (Blair *et al.* 1998). Therefore it is probable that evolutionary processes have selected bunchgrasses for growth traits that respond to the low level of nitrogen in the environment, at the expense of growth processes which would be required if nitrogen were non-limiting. Hence a model that ignores the effect of nitrogen on clonal tiller growth would probably miss a fundamental component that ensures the stability of bunchgrass systems.

Daily soil nitrogen available to plants is restricted and seasonal (Knapp *et al.* 1998). The maximum rate of nitrogen uptake from the soil, RNuptake, is set to $0.01g\,N\,(g\,wlr)^{-1}\,d^{-1}$ for the months July to November and then declines to zero through December, and remains zero for the remainder of the year. This period of nitrogen availability was chosen to mimic the high availability of soil nitrogen during spring and early summer relative to other parts of the year in humid grasslands growing in summer rainfall areas, because of nitrogen inputs from thunderstorm activity during this period and nitrogen from the accumulated decay of soil matter over the previous winter (Blair *et al.* 1998). In reality soil nitrogen availability is far less blocked and actually occurs as a series of pulses in response to environmental cues, particularly rainfall events and changes in soil water potential (Birch 1958; Campbell & Grime 1989; Blair *et al.* 1998).

3 ASSESSING THE PERFORMANCE OF GROWTH STRATEGIES

The multiple tiller model generates a large amount of information. In order to analyse the effects of different growth strategies it is necessary to make a list of criteria that can be used to assess the behaviour of the modelled clones. Interpreting the raw data across the entire simulation is difficult because of the number of data points. Therefore the data must be

summarised appropriately to provide relevant information. There are two components to this problem. The first component relates to the seasonal behaviour of the clone under different growth strategies. Intra-annual behaviour can be assessed by averaging daily growth values for each day of the year ('Yearday') across the years of the simulation. The second component relates to the success of a growth strategy in capturing and holding resources. This is most easily represented by averaging summed annual values across the years of the simulation. The following behaviours and parameters were considered:

1. Stability
    a. Does the system self-perpetuate for the length of the simulation? Alternatively does it collapse?
    b. Are there inter-annual patterns of growth (e.g. cyclicity)?
2. Average intra-annual growth patterns
    a. Average daily live object number
    b. Average daily live root biomass (g), live shoot biomass (g), root-to-shoot ratio
    c. Average daily AVC (g CHO) and AVN (g N)
3. Individual production parameters
    a. Number of flowering tillers
    b. Average maximum blade-, sheath-, internode- and flower mass of flowering tillers
    c. Average annual summed net photosynthesis (g CHO)
    d. Average annual summed nitrogen absorption (g N)
    e. Average annual summed growth (g CHO)
    f. Average annual summed growth deficit (g CHO)

The model runs by initiating a clone consisting of one tiller. This tiller recruits secondary tillers and subsequently new ramets and ramet groups are formed. It takes time for the clone to occupy the system space defined by the model constraints on resources. Therefore the first five years of data are ignored for both averaging methods in order to ignore values generated by the model while the clone grows to occupy the given space. For the simulations conducted here this length of time was reasonable because most clones had filled the available space within this period.

All multiple tiller simulations conducted in this thesis were set to run for 10 000 day iterations (i.e. just over 27 years).

Regulation of intra-clonal growth in bunchgrasses is poorly understood (Derner & Briske 1999). It is apparent that young tillers on individual ramets may die even during periods of active growth on perennial bunchgrasses (Tainton & Booysen 1965; Tomlinson & O'Connor 2005). This indicates that resource allocation is disproportionate across physiologically integrated ramets.

The most probable explanation for disproportionate allocation among sinks is that passive termination may occur because restricted resources are directed towards larger sinks (Bangerth 1989) which results in a positive feedback loop that starves smaller sinks and ultimately terminates them. This process underlies what is termed apical dominance. Bangerth's theory of auxin-induced auto-inhibition of lateral shoots proposes that the ability of a shoot to attract resources for its continued growth and development depends on its auxin output relative to other shoots (Bangerth 1989, Bangerth et al. 2000). Presumably auxin production is related to photosynthetic activity. By this means resources get directed to the most photosynthetically-active shoots and away from less active shoots and side-shoots. During periods of resource-limited growth this disproportionate allocation ensures that smaller shoots die back more than they grow, eventually killing them.

Disproportionate allocation between tillers presumably improves resource allocation efficiency across a ramet because it promotes the growth of more productive structures and therefore improves the supply of resources (Sachs, Novoplansky & Cohen 1993). Essentially this implies that disproportionate allocation may be an adaptation for spatial heterogeneity in resource availability of sun-grown plants (Hutchings & de Kroon 1994).

However no researchers appear to have anticipated that another important role of disproportionate allocation may be to improve temporal resource allocation efficiency. Consider proportionate allocation versus disproportionate allocation between tillers. If resource allocation is based strictly proportionately on the growth demand of individual tillers then proportionately all are equally compromised when available resources are limiting to growth, and relatively fewer will be terminated under those conditions. Hence ramet growth at all future times would still be allocated relatively inefficiently to all live tillers thus slowing the rate at which individual tillers recover after periods of critical resource limitation. Disproportionate allocation would remove less-efficient tillers more rapidly and reduce the total demands placed by the ramet for resources during resource-

limited periods, thereby increasing the rate at which individual tillers overcome resource limitation after growth-limiting periods. However it is unclear what effect the shift from proportionate to disproportionate allocation will have on total clonal growth. Specifically, does disproportionate allocation improve or reduce total clonal growth over that achieved by clones with proportionate growth? If it is the former, then we can predict that all bunchgrasses should favour disproportionate allocation regardless of environment. If it is the latter, then there is a trade-off between individual tiller growth and clonal growth, which may be associated with different growth strategies employed by bunchgrass species.

In this section the effect of proportionate and disproportionate allocation to tillers and ramets is explored using the TILLERTREE model. The following questions are asked:

1.	Are there differences in the growth patterns of clones grown with proportionate allocation and disproportionate allocation?

2.	Do these differences result in differences in ability to capture and utilise environmental resources?

## 4.1	Model rules for resource allocation

Disproportionate resource allocation within tiller ramet groups can be defined at two levels, namely the tiller level and the ramet level. Resource allocation in plants is a semi-continuous process with both carbohydrates and minerals being moved by mass flow in the phloem and xylem. In addition there may be some resistance to the flow of resources among tillers and particularly among connected ramets (see models described by Thornley & Johnson 1990). This increases the complexity for a discretely-structured model like the present one, where simplified rules are necessary to define the movement of resources among connected objects. The model assumes that if there are sufficient resources to feed the entire ramet group, then exact demands are supplied to each ramet and the excess is allocated by live mass. The problem of disproportionate allocation arises when there are insufficient resources to feed all sink demands completely.

All vegetative shoot growth, either at ramet or tiller level, is directed to maximise photosynthetic production. Therefore in each iteration ramets are ordered in terms of their net photosynthetic production and resources can be allocated in order from most productive to least productive. This means that resources can be allocated preferentially to the ramets with the highest photosynthetic production. Similarly at the tiller level, all tillers on a

particular ramet are ordered in terms of their net photosynthetic production and resources are allocated to tillers in the same preferential manner. This is a greedy algorithm. In the completely greedy case, the ramet will get as much of the resource as it requires as long as there is sufficient resource available to do so. In the completely proportionate case, a ramet will get allocated carbohydrate and nitrogen in proportion to its demand relative to total demand of the ramet group. The strength of the greediness is manipulated by the 0-1 allocation parameter, A, which shifts the allocation between the two extremes. If A = 1 then allocation is proportionate, if A = 0 then allocation is greedy, if $0 < A < 1$ allocation is disproportionate. Hence carbohydrate allocation among ramets on the same ramet group depends on A_γ and available resources.

$$\Psi Calloc_{\gamma,\delta,t} = A_\gamma \frac{Demand_{\gamma,\delta,t}}{\sum_\gamma Demand_{\gamma,\delta,t}} + \left(1 - A_\gamma\right) Demand_{\gamma,\delta,t} \qquad 8.3$$

$$AVC_{\gamma,\delta,t} \;\; += \;\; min\left(GrowC_{\delta,t} \; ; \Psi Caloc_{\gamma,\delta,t}\right). \qquad 8.4$$

Allocation among tillers on the same ramet is structured similarly, using A_β.

$$\Psi Calloc_{\beta,\gamma,\delta,t} = A_\beta \frac{Demand_{\beta,\gamma,\delta,t}}{\sum_\gamma Demand_{\beta,\gamma,\delta,t}} + \left(1 - A_\beta\right) Demand_{\beta,\gamma,\delta,t} \qquad 8.5$$

$$Calloc_{\beta,\gamma,\delta,t} = min\left(AVC \; ; \Psi Caloc_{\beta,\gamma,\delta,t}\right). \qquad 8.6$$

It is presently assumed that disproportionate allocation only affects resources allocated to growth. In other words, both maintenance demands and storage demands are shared proportionately across all ramets and tillers. Hence all tillers are equally compromised if available carbohydrate resources are so low that the maintenance requirement of the ramet group is not satisfied. This would not be strictly true if resource allocation is driven completely by sink demands, in which case allocation among sinks is determined by the sum of maintenance, storage and growth demands of that sink. However the approach

adopted here is more conservative in order to prevent object termination when total resource availability may only limit growth marginally. The present method still leads to disproportionate allocation that should compromise smaller and/or less productive objects when resources are limiting to growth. This method also ensures that older tillers carrying secondary tillers are provided with carbohydrate for maintenance and therefore are not terminated even they only consist of live stem material.

If the resource availability of the system exceeds the total demands of the system for a particular resource, this excess is divided proportionately among all the ramets on the basis of their live mass. This ensures that the excess resource concentration is equal in all ramets. Excess resources are only allocated to ramets after maintenance, storage and growth requirements have been satisfied.

$$\Delta AVC_{\gamma,\delta,t} = \frac{wltr_{\gamma,\delta,t}}{\sum_{\gamma} wltr_{\gamma,\delta,t}} Cexcess_{\delta,t} .$$

8.7

4.2 Simulated strategy: equally disproportionate allocation at ramet and tiller levels

The rules for resource allocation among live structures on clones defined above indicate that the level of disproportionate allocation between ramets and the level of disproportionate allocation between tillers could differ. A number of researchers have emphasised that resource allocation can be affected by flow resistance (Thornley & Johnson 1990), and lateral movement between ramets may be more difficult than vertical movement between tillers. However these differences are not well-understood and creating differences in disproportionate allocation applied at each level will complicate the behaviour. Therefore for the analysis conducted here each clone was grown with the same level of disproportionate allocation applied at the tiller and ramet levels ($A_\gamma = A_\beta$), as this assumed an equal level of bias in allocation among ramets on the same ramet group and among tillers on the same ramet. This meant the most productive tiller on the most productive ramet within a ramet group would have its demands best satisfied on any given day.

The assumptions underlying the strategy are as follows:

- there is unrestricted movement of mobile resources both within and among individual ramets
- allocation to sinks is not limited by distance effects
- the level of disproportionate distribution of resources is solely determined by the values of A_γ and A_β.

4.3 Procedure

The model simulated the growth of a clone using proportionate allocation ($A_\gamma = A_\beta = 1.00$) for 10 000 iterations. Then the model was rerun with clones using disproportionate allocation with different values for the allocation parameters A_γ and A_β, but where A_γ was always set equal to A_β (disproportionate allocation strategy 1). The values of A_γ and A_β used were 1.00, 0.75, 0.50, and 0.25.

4.4 Results

Figures 8.1 and 8.2 show the daily data for live objects and leaf area index (LAI) as generated by the model for the proportionate clone ($A_\gamma = A_\beta = 1.00$) and the least disproportionate clone ($A_\gamma = A_\beta = 0.75$). The other disproportionate strategy clones behaved similarly to the least disproportionate clone, so these are not shown.

The clones grew quite quickly to fill the available space within about three years. Importantly all clones survived for the entire 10 000 iterations, indicating that all are able to persist. The seasonal pattern of growth is apparent as represented by the regular annual spikes in data around the flowering period, which reflects the availability of environmental resources as well as the seasonal development of *Themeda triandra* tillers. Neither proportionate nor disproportionate clones exhibited inter-annual cyclicity.

There was a greater amount of inter-annual variation for the proportionate clone than for the disproportionate clones. This indicates that there are large carry-over effects on the seasonal behaviour caused by the discrete changes in live object number of the clone and delays in the decay of dead biomass. Inter-annual variation in the live object number and LAI was reduced on the disproportionate clones, indicating that disproportionate allocation

Figure 8.1 Number of live tillers (————), live ramets (— — —) and live ramet groups (· · · · ·) recruited and surviving on a clone of the modelled grass *Themeda triandra*. a. Proportionate allocation ($A_\gamma = 1.00$, $A_\beta = 1.00$); b. Disproportionate allocation ($A_\gamma = 0.75$, $A_\beta = 0.75$). (Environmental conditions: Plant activity during the growing and non-growing season as defined in Section 4.3 of Chapter 4. Growing season proceeds from Yearday 1 to Yearday 242 of each year. Daily soil nitrogen availability as described in Section 3 of Chapter 4.)
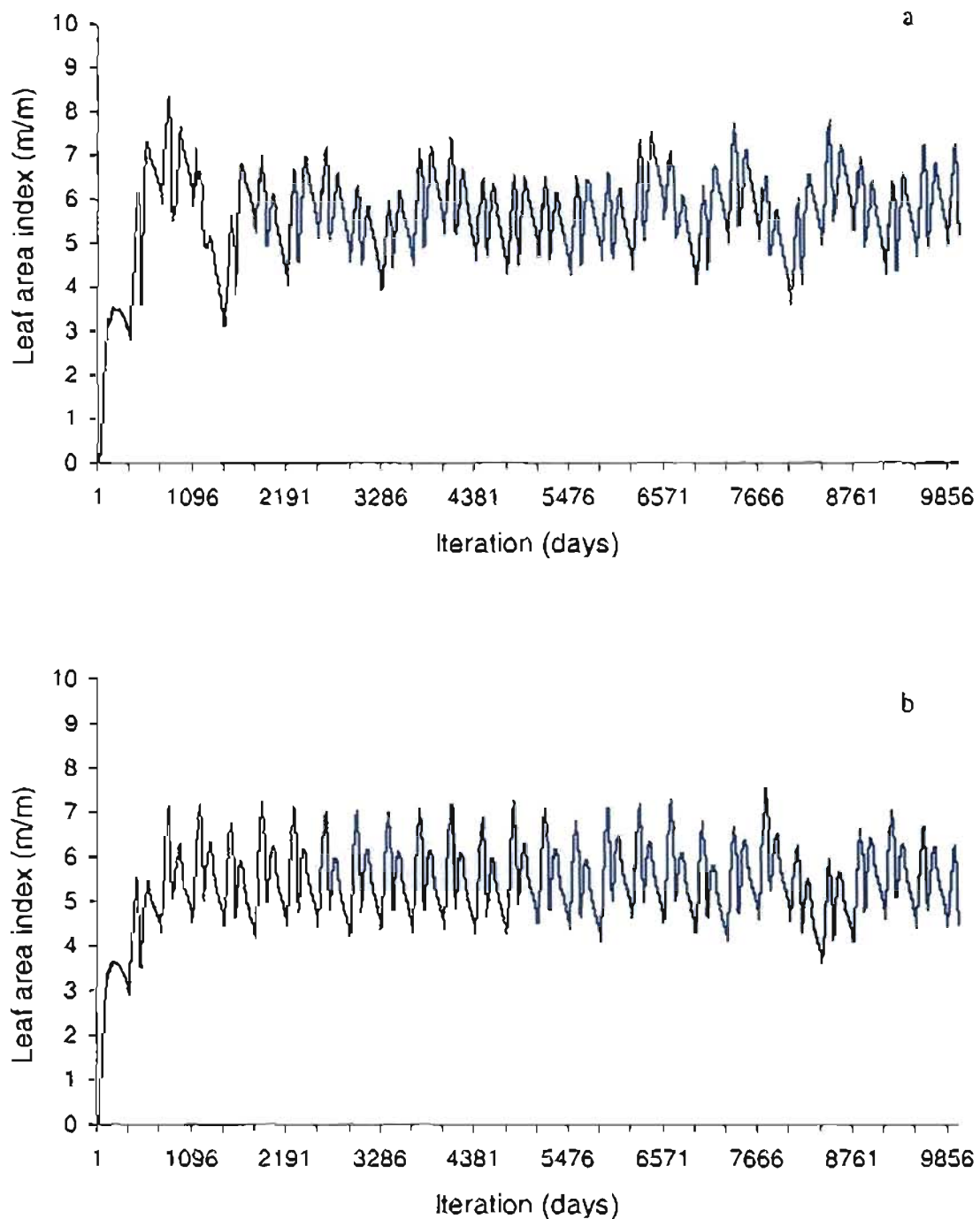
Figure 8.2   Leaf area index (LAI) at ground level of a clone of the modelled grass *Themeda triandra*. a. Proportionate allocation (A_γ = 1.00, A_β = 1.00); b. Disproportionate allocation (A_γ = 0.75, A_β = 0.75). (Environmental conditions: Plant activity during the growing and non-growing season as defined in Section 4.3 of Chapter 4. Growing season proceeds from Yearday 1 to Yearday 242 of each year. Daily soil nitrogen availability as described in Section 3 of Chapter 4.)

reduces the inter-seasonal variation caused by discrete growth processes once the clone has occupied the available resource space. However, it is clear that the proportionate clone grows more quickly during the first two seasons than the disproportionate clone indicating that it is better able to accumulate resources during the early colonisation phase of the model.

Live object number

The average live number of objects on each clone each day in a year is given in Figure 8.3. The number of live objects mainatained across a year was highest on the proportionate clone and decreased across the clones as the level of disproportionate allocation increased.

Average live tiller, ramet and ramet group numbers followed similar seasonal patterns on all four clones. The number of ramets and the number of tillers remain very close together at certain times of the year, indicating that there is a consistent turnover in live tillers which senesce after they have completed flowering. This was because all basal tillers were able to root and become independent structures.

The seasonal tiller recruitment patterns were similar across all clones with two tiller recruitment periods, the first during early spring and a second, larger recruitment during the post-flowering period. Absolute recruitment was highest on the proportionate clone and decreased as the level of disproportionate allocation increased, but the relative size of the tiller recruitment (tillers recruited per parent tiller) during the post-flowering period was similar across the clones.
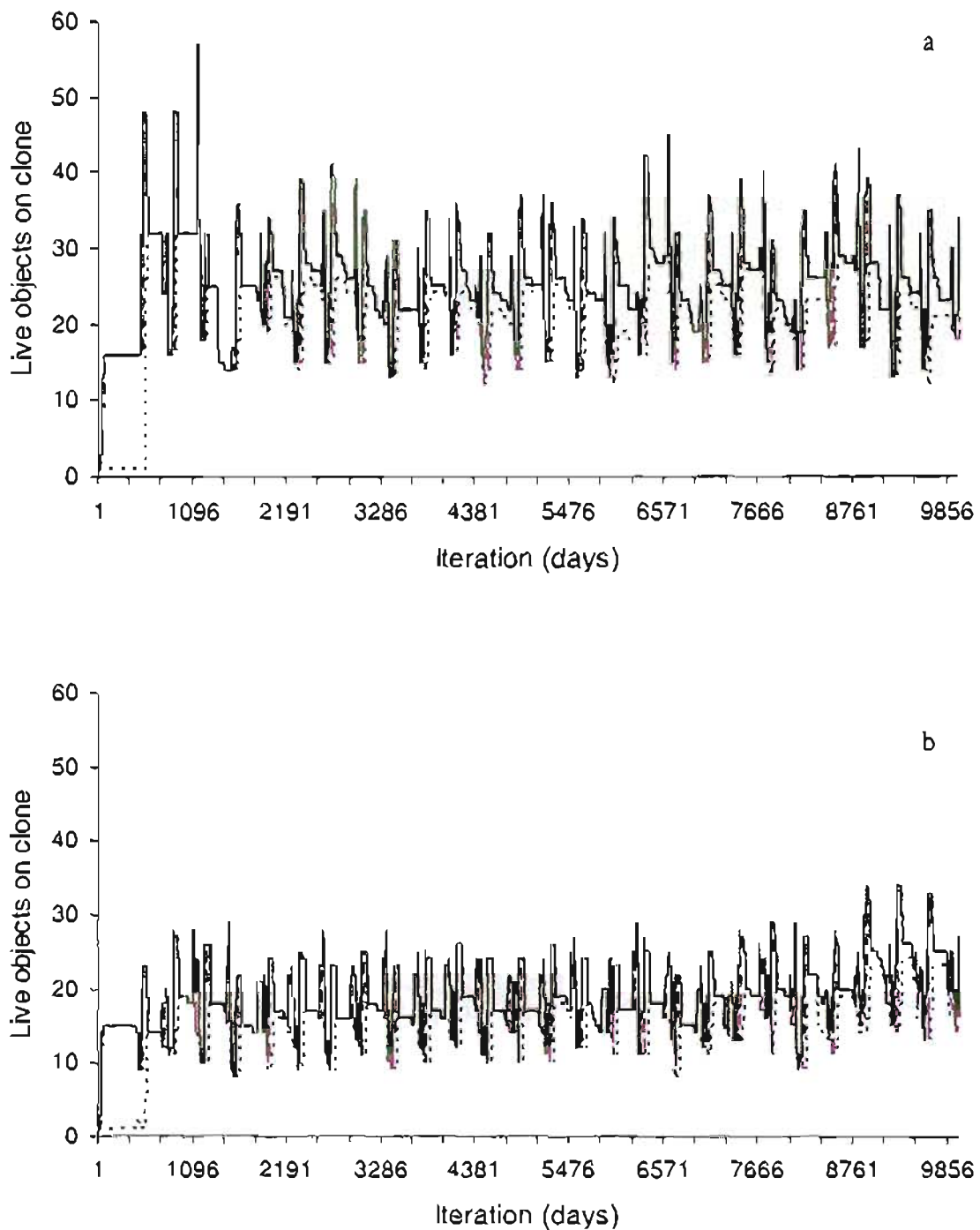
124
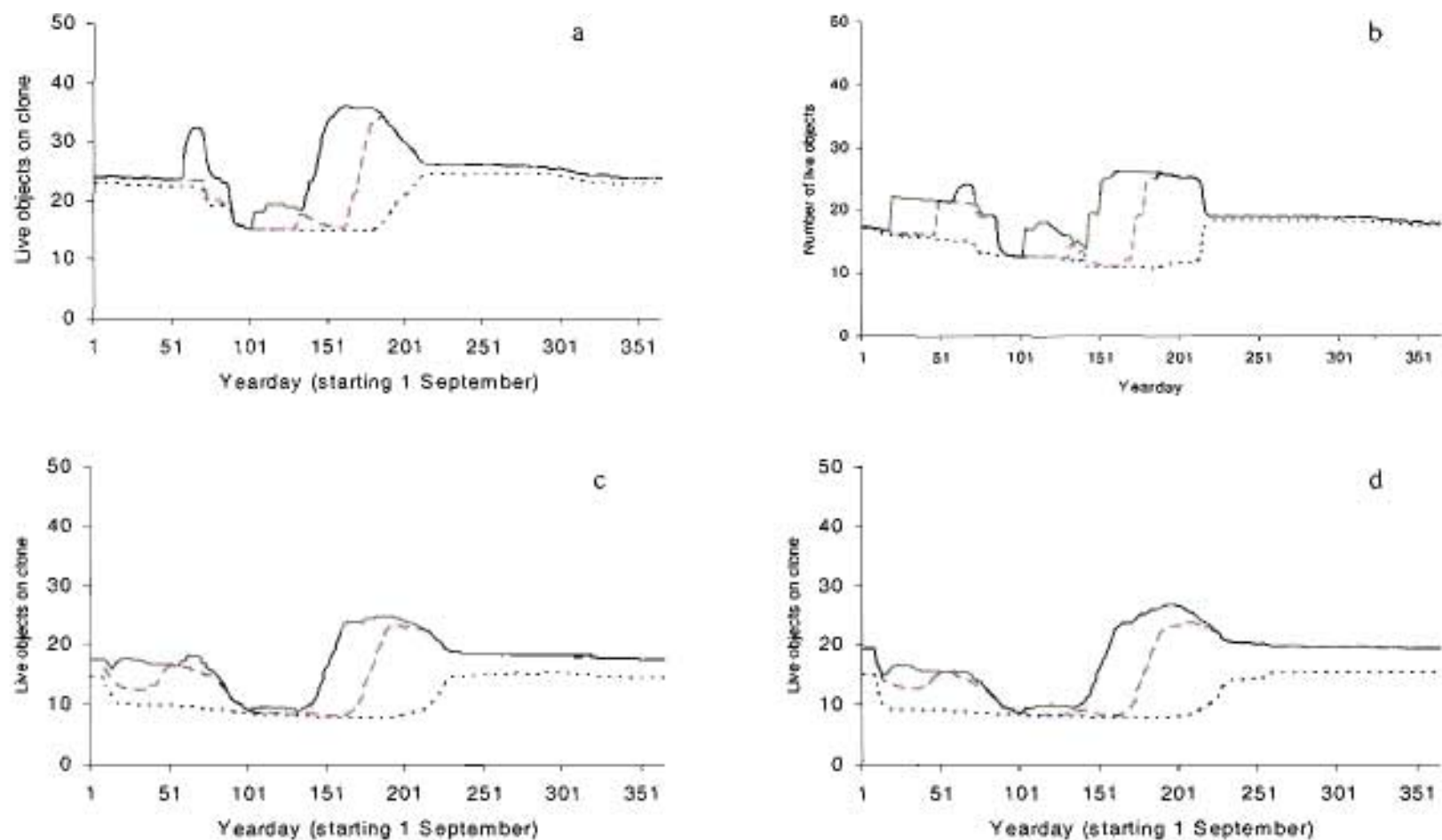
Figure 8.3 Average clonal daily number of live tillers (————), live ramets (— — —) and live ramet groups (· · · · ·) recruited and surviving on a clone of the modelled grass *Themeda triandra*, for four allocation procedures. a. Proportionate allocation ($A_\gamma = 1.00$, $A_\beta = 1.00$); b. Disproportionate allocation ($A_\gamma = 0.75$, $A_\beta = 0.75$); c. Disproportionate allocation ($A_\gamma = 0.50$, $A_\beta = 0.50$); d. Disproportionate allocation ($A_\gamma = 0.25$, $A_\beta = 0.25$). (Environmental conditions: Plant activity during the growing and non-growing season as defined in Section 4.3 of Chapter 4. Growing season proceeds from Yearday 1 to Yearday 242 of each year. Daily soil nitrogen availability as described in Section 3 of Chapter 4.)

Table 8.1 Average annual performance of modelled clones of *Themeda triandra* with different growth resource allocation ratios which are applied both at ramet level and tiller level

	Allocation procedure							
	Proportionate		Disproportionate		Disproportionate		Disproportionate	
	$A_\gamma = 1.00, A_\beta = 1.00$		$A_\gamma = 0.75, A_\beta = 0.75$		$A_\gamma = 0.50, A_\beta = 0.50$		$A_\gamma = 0.25, A_\beta = 0.25$	
	Mean	S.E.	Mean	S.E.	Mean	S.E.	Mean	S.E.
Average reproductive tiller data								
Number of flowering tillers	9.09	0.366	7.09	0.020	5.95	0.27	5.95	0.22
Maximum blade mass (g tiller^{-1})	0.091	0.003	0.126	0.003	0.137	0.003	0.139	0.003
Maximum sheath mass (g tiller^{-1})	0.027	0.001	0.043	0.001	0.052	0.002	0.053	0.002
Max internode mass (g tiller^{-1})	0.153	0.005	0.214	0.005	0.271	0.008	0.272	0.008
Maximum flower mass (g tiller^{-1})	0.030	0.001	0.041	0.001	0.052	0.002	0.051	0.002
Maximum culm length (mm)	428.47	10.85	564.07	12.41	681.35	17.19	680.43	18.85
Average clonal organ mass								
Maximum blade mass (g)	0.936	0.024	1.082	0.021	0.865	0.029	0.883	0.024
Maximum sheath mass (g)	0.272	0.008	0.336	0.005	0.319	0.010	0.326	0.007
Maximum internode mass (g)	1.381	0.043	1.512	0.018	1.586	0.047	1.596	0.034
Maximum flower mass (g)	0.264	0.007	0.285	0.004	0.304	0.009	0.297	0.007
Average clonal annual production								
Net photosynthesis (g CHO)	18.488	0.328	19.337	0.159	18.280	0.363	18.177	0.303
N absorption (g N)	0.106	0.001	0.101	0.001	0.093	0.002	0.091	0.002
Summed growth (g CHO)	13.330	0.237	13.683	0.094	13.117	0.266	13.094	0.221
Summed growth deficit (g CHO)	117.278	2.185	122.242	2.014	84.516	3.416	87.620	3.411

Resource capture and growth .

The average summed annual net photosynthesis, root nitrogen absorption, growth and growth deficit (growth demanded by structures but not satisfied) for the clones employing each of the four strategies respectively are given in Table 8.1. The proportionate clone and least disproportionate clone ($A\gamma = A\beta = 0.75$) achieved greater production, net photosynthesis and root nitrogen absorption, and growth deficit than the two more disproportionate clones. Notably root nitrogen absorption decreased across the clones as the level of disproportionate allocation increased. The greater resource acquisition and production achieved by the proportionate and least disproportionate clones was due to the fact that these clones maintained more live tillers during early spring when soil nitrogen was highest. These two clones also had the greatest growth potential, which is indicated by their greater actual growth and growth deficit values. The least disproportionate clone actually had greater annual photosynthesis and growth than the proportionate clone, which indicates that directed resource allocation improved the growth of the least disproportionate clone but restricted the growth of the more disproportionate clones relative to growth and photosynthesis on the proportionate clone.

Seasonal patterns of root and shoot growth

The seasonal live shoot mass, live root mass, and root-to-shoot ratio are presented in Figure 8.4. These indicate that there was substantial growth during spring and that biomass peaked during flowering. After this period live mass dropped substantially as the reproductive tillers died and smaller tillers that were recruited in response to increased availability of nitrogen and carbohydrate (Figure 8.5) started to expand.

The root-to-shoot ratios on all clones increased during the early spring period, indicating that nitrogen is more limiting to growth at this time. However the root-to-shoot ratios declined again as AVC becomes more restrictive. Carbohydrate and nitrogen were limiting during stem elevation and flowering due to the large daily growth demands for resources placed during this period. After flowering, the root-to-shoot ratio increased (about Yearday 125) because reproductive tillers died back rapidly while the roots responded slowly to the decline in shoot biomass. The small size of secondary tillers during the post-flowering period meant that photosynthetic production was highly restricted at this time.

126
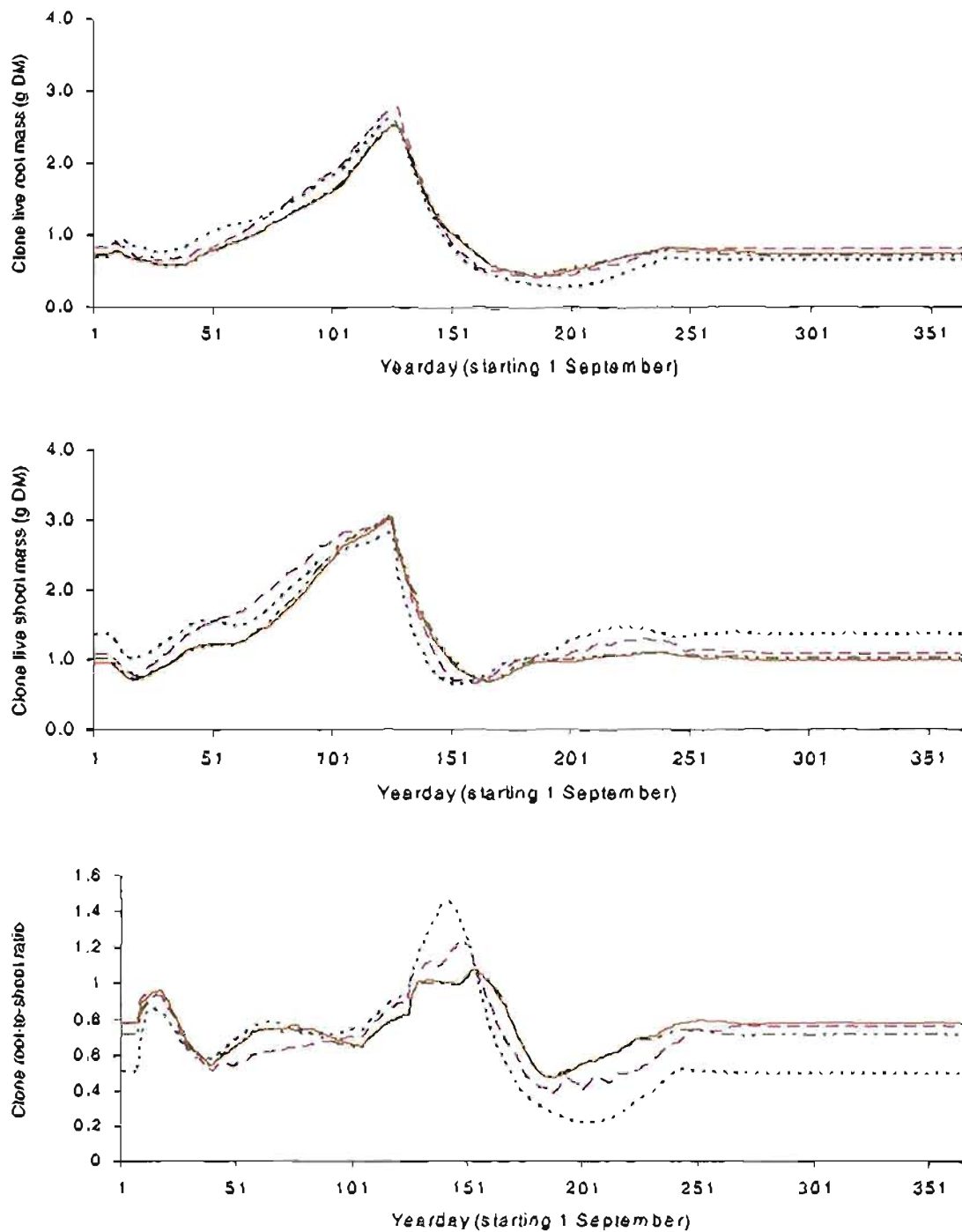
Figure 8.4 Average clonal daily live shoot mass, live root mass and R:S ratio for a clone of the modelled grass *Themeda triandra*, for four allocation procedures. ($\cdots\cdots$ Proportionate allocation ($A_\gamma = 1.00$, $A_\beta = 1.00$); $-\,-\,-$ Disproportionate allocation ($A_\gamma = 0.75$, $A_\beta = 0.75$); $\underline{\quad\quad}$ Disproportionate allocation ($A_\gamma = 0.50$, $A_\beta = 0.50$); $-\,\cdot\,-$ Disproportionate allocation ($A_\gamma = 0.25$, $A_\beta = 0.25$).) (Environmental conditions: Plant activity during the growing and non-growing season as defined in Section 4.3 of Chapter 4. Growing season proceeds from Yearday 1 to Yearday 242 of each year. Daily soil nitrogen availability as described in Section 3 of Chapter 4.)
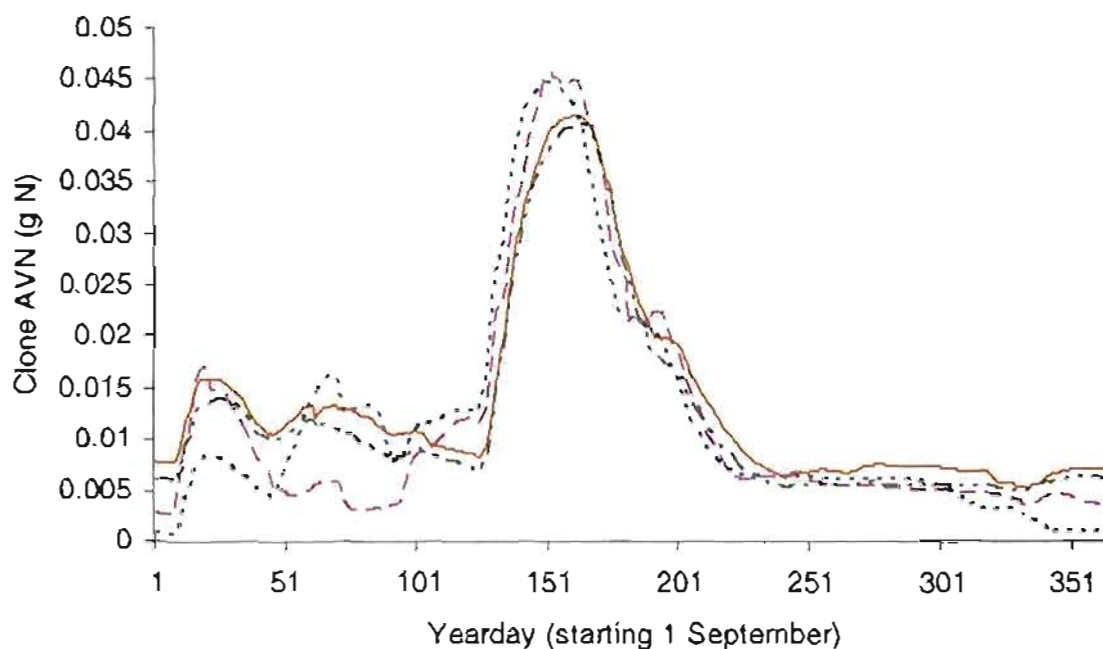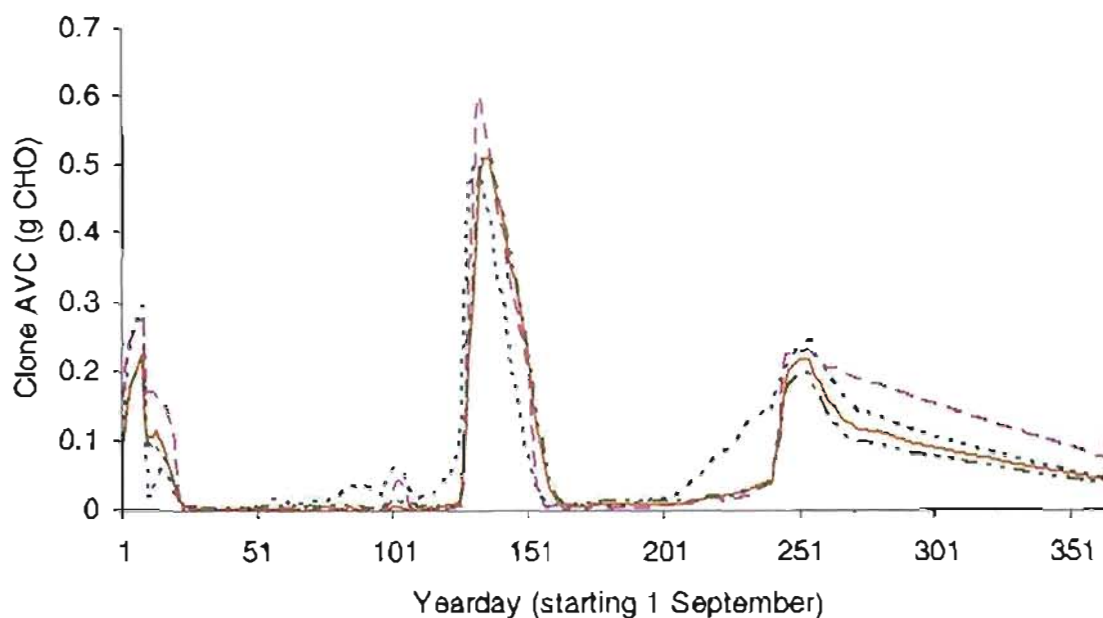
Figure 8.5 Average clonal daily available non-structural carbohydrate (AVC) and available non-structural nitrogen (AVN) for a clone of the modelled grass *Themeda triandra*, for four allocation procedures. (· · · · · · Proportionate allocation ($A_\gamma = 1.00$, $A_\beta = 1.00$); — — — Disproportionate allocation ($A_\gamma = 0.75$, $A_\beta = 0.75$); ———— Disproportionate allocation ($A_\gamma = 0.50$, $A_\beta = 0.50$); — · · — Disproportionate allocation ($A_\gamma = 0.25$, $A_\beta = 0.25$).) (Environmental conditions: Plant activity during the growing and non-growing season as defined in Section 4.3 of Chapter 4. Growing season proceeds from Yearday 1 to Yearday 242 of each year. Daily soil nitrogen availability as described in Section 3 of Chapter 4.)

This in turn ensured that more resources were allocated to shoot growth in order to improve the photosynthetic output, so root-to-shoot ratios fell substantially until sufficient photosynthetic surface has been established on the new tillers to overcome this deficit. Hence the root-to-shoot ratio increases again by the time the non-growing season begins on Yearday 243.

Absolute differences in average daily live biomass among the four clones were quite small but there are still patterns to be noted (Figure 8.4). The proportionate clone and least disproportionate clone had higher root and shoot biomass than the disproportionate clones during the spring regrowth period, which allowed them to capture more nitrogen than the other clones. However in the post-reproductive period the root biomass of the proportionate clone was below that for the disproportionate clones while its shoot biomass remained higher than for the disproportionate clones. The root-to-shoot ratio of the proportionate strategy underwent dramatic shifts from the end of flowering through to the end of autumn relative to the disproportionate strategies. Changes to the root-to-shoot ratio of each clone decreased across the clones as the level of disproportionate allocation increased. This was because disproportionate resource allocation favoured the growth of the most photosynthetically productive shoots, which increased the rate at which disproportionate clones overcame light limitation by expanding fewer leaves more quickly through the overlying canopy than more proportionate clones. The inefficiency of resource allocation on the proportionate clone caused its root-to-shoot ratio to decline substantially relative to the other clones during the post-flowering period, as it attempted to re-establish shoot photosynthetic surface by expanding all live tillers in proportion to their demands.

Clonal shoot performance and individual tiller performance

Average maximum reproductive tiller organ masses for each allocation strategy are presented in Table 8.1. The data indicates that the size of organs on individual reproductive tillers increased with increasing greediness employed by the clone, although the number of flowering tillers decreased with increasing greediness. Thus individual tiller performance improved with increasing greediness, because more resources were allocated to the most photosynthetically productive tillers which resulted in fewer, larger tillers surviving to sexual reproduction.

Average annual maximum clonal live blade, sheath, internode and flower masses for each allocation strategy are presented in Table 8.1. As expected from the previous sections, the greatest growth was achieved by the least disproportionate strategy ($A\gamma = A\beta = 0.75$). Both the proportionate clone and the least disproportionate clone achieved greater leaf biomass than the two more disproportionate clones, but the latter achieved greater stem (internode) masses and floral masses, indicating that the improved performance of individual tillers under disproportionate allocation over-compensated for the reduction in floral number.

4.5   Discussion

The simulations indicate that there are differences in the growth patterns of bunchgrass clones with different levels of disproportionate allocation, which indicate a trade-off between individual tiller growth and clonal growth. The proportionate clone maintained more live objects than the more disproportionate clones, which maintained less live objects as the level of disproportionate allocation increased. This confirms that disproportionate allocation adjusts the temporal resource allocation towards more productive structures (Sachs et al. 1993). Consequently individual tiller size was smallest on the proportionate clone and increased across the disproportionate clones as the level of disproportionate allocation increased. Intra-annual clonal growth was more variable on the proportionate clone than on disproportionate clones. Growth and productivity were higher on least disproportionate clone and the proportionate clone than on the two more disproportionate clones. The former two clone were more successful at capturing and utilising available resources because they maintained a larger numbers of live tillers, which allowed them to expand more quickly when conditions were suitable for growth even though individual tiller growth was reduced. The more disproportionate strategies maintained fewer live tillers and hence had reduced ability to utilise periods of high nitrogen availability because of restrictions on growth potential. However individual tiller growth during flowering was substantially better on the more disproportionate clones because more resources could be directed to them because there were fewer tillers competing for resources and fewer reproductive tillers. The improved growth of individual tillers enabled them to achieve greater total flower masses then the proportionate clone and least disproportionate clone.

In simulations with fewer, thicker LAI layers, the difference in growth and resource capture among more proportionate and less proportionate clones increased, so that total

clonal flower mass on less disproportionate clones increased above that achieved by more disproportionate clones, suggesting that the trade-off between individual tiller performance and clonal performance can affect total seed production. Clearly this occurred because of the improved light availability in lower portions of the canopy. It is plausible that this effect is not expressed under the simulations presented here, because the LAI model presented in this thesis assumes that leaves on the bunchgrass clones remain vertical in the canopy after death, whereas in reality they bend over and curl up thereby allowing more light to penetrate through the canopy, reducing photosynthetic limitation in the top half of the canopy. This process will be explored in future extensions to the model.

A trade-off between individual tiller growth and total clonal growth and soil nitrogen capture suggests that the level of disproportionate allocation may be associated with different growth strategies employed by higher plants. Species following more proportionate allocation will produce many–branched structures that result in a large number of inflorescences per plant. Each inflorescence may be small in size, but total seed production could potentially be large. Species following more disproportionate allocation will produce fewer inflorescences per plant although the average size of these inflorescences will be large, so total seed number production across the plant may be reduced. Individual shoot growth will be reduced (both height and mass) on more proportionate plants meaning that these plants will be less-well adapted to cope with light competition because individual shoots will be shorter, and therefore could be outcompeted by species with more disproportionate allocation that grow fewer, larger shoots more rapidly. This in turn may point to a fundamental difference in the allocation strategies employed by r-strategist and K-strategist plants in general (MacArthur & Wilson 1967). The r-strategists may favour more proportionate resource allocation in order to maximise biomass growth rate and ensure maximum seed production in the short term, because they increase in non-light-competitive environments where quantity of growth and resource capture is more important than individual shoot performance. They grow more quickly during the first few seasons of growth, as demonstrated by the proportionate clone (Figure 8.1), allowing them to colonise resources rapidly, but their subsequent growth is unstable as resources become rare, making them more susceptible to severe dieback during resource-limiting periods. The K-strategists may favour more disproportionate resource allocation because this improves the growth of individual shoots (quality) in light-competitive environments, but at the expense of total seed production potential. The strategy also

favours the growth of large individual seeds because there is less competition for resources between shoots across the plant.

As disproportionate allocation can promote individual shoot growth and individual seed size, this would suggest that disproportionate allocation may be selected by plants in response to two types of environmental problem, increased competitive ability in light-limited environments and increased seed size to promote survival of seedlings in environments restricted by some environmental resource. This means that seed size may sometimes have evolved complementarily with increased shoot size in light-limited environments to promote seedling growth in response to the same resource limitation. Alternatively, disproportionate shoot growth may have been selected to promote seed size in environments with restricted soil nutrients. Westoby, Leishmann & Lord (1996) reviewed the evidence on seed size across plant forms and concluded that increased seed size must be chosen in order to increase reserves available to the new seedling. They further stated that the available evidence suggested that large seed size was chosen as a response to light limitation only, but pointed out that responses to soil nutrients had hardly been investigated. It still seems probable that species growing in nutrient-poor soils would be competitively advantaged if their seedlings have an increased chance of establishing because they have access to a larger pool of reserve nitrogen. I suggest that one problem with the approach taken by Westoby et al. (1996) is that they consider seed size across growth forms, whereas it may be more insightful to consider seed size variation within growth forms, given that seed size between growth forms can differ by orders of magnitude (e.g. ramets versus bunchgrasses).

So what evidence is there from grasses? Annual grass species growing in environments that are limited by soil nutrient acquisition and water restrictions produce copious amounts of small seeds to ensure regrowth in the next growing season and therefore individual tiller performance is not a requisite for their success. Annual grass species often form many-branched structures during their season-long life-cycles (Beard et al. 1978; Young et al. 1987) in order to maximise the number of flowering structures. In terms of the above results it would seem likely that annual plants could follow a more proportionate allocation of resources to shoots to maximise the growth rate in order to maximise soil nutrient capture and subsequent seed production. However there are annual grass species, for example Urochloa mosambiciensis, that have larger seeds and fewer, larger shoots. The species grows across soil fertility gradient in semi-arid areas, so selection for nutrient-poor soils seems unlikely as an explanation for fewer shoots. The reduced shoot number may

reflect increased organ growth rates and consequently reduced tiller recruitment (Tomlinson & O'Connor 2005), which indicates that there are confounding processes. However, it should be simple enough to determine whether the species allocates resources more or less proportionately between tillers by determining the proportion of tillers that die prematurely on plants during the growing season.

More proportionate allocation may also be employed by short perennial species growing in environments where light is non-restrictive, for example species growing on very shallow soils. In these environments no benefit is obtained by being selective in tiller survival, because growing periods are severely restricted, so the species remain quite short and consequently blade photosynthesis is not limited by overshading. Grass species growing in more enclosed environments require better individual tiller growth in order to compete for light (see Chapter 7). This suggests bunchgrass species growing in light-limited humid grasslands would follow a more disproportionate allocation strategy in order to promote individual growth. This would also result in fewer inflorescences, but with larger individual size. This has been recorded for Themeda triandra, a species which is dominant in humid mid- to tall grasslands in Africa, for which a small proportion of the tillers recruited on each bunchgrass clone actually flower (Tainton & Booysen 1965; Coughenour et al. 1985). Themeda triandra also produces seeds that are heavier than most other competitor bunchgrass species in the Southern Tall Grassveld (O'Connor & Bredenkamp 1997). However Themeda triandra is outcompeted in irregularly defoliated swards in the Southern Tall Grassveld by a taller, faster-growing species, Eragrostis curvula (Fynn et al. 2005a; Tomlinson & O'Connor 2005), which is noted for its large inflorescences with many small seeds (Field-Dodgson 1976). The latter suggests that large seed size is not a prerequisite for competitive success in light-limited humid grasslands in contrast to the conclusions of Westoby et al. (1996), and that competitive ability of tillers on clones is more critical.

The arguments presented here on more proportionate versus more disproportionate tiller growth have relevance to the more general concept of apical dominance in higher plants. Plant species have sometimes been classified in the relative sense as exhibiting 'strong' or 'weak' apical dominance (Cline 1991). Apical dominance has often been incorrectly misconstrued as responsible for inhibition of lateral shoots, which is more likely to be controlled by temporal and localised resource availability (Tomlinson & O'Connor 2004). In this sense some species perceived to exhibit 'strong' apical dominance because they exhibit little lateral shoot growth are only demonstrating the effects of resource limitation which accompanies their relatively fast growth rates (Cline 1994; Sadras & Fitt

131

1997). It is more correct to associate apical dominance with resource competition between existing shoots (Bangerth 1989). In this sense 'strong' apical dominance may be associated with more disproportionate resource allocation between connected shoots, while 'weak' apical dominance may be associated with less disproportionate resource allocation between shoots. Thus the strength of apical dominance depends on the rate at which resources may be directed away from less attractive shoots towards more attractive shoots. This in turn will depend on two things: individual shoot growth rates and relative ability to attract resources as determined by some signal from the shoot, presumably auxin (Cline 1994; Bangerth et al. 2000). Consider a plant with two shoots that are identical and growing in identical environments. We can assume that they have identical shoot growth rates and are able to attract equal amounts of the available pool of resources. Suppose now the second shoot is placed in a shaded environment. Then the plant will adjust for this by allocating more resources to the shoot growing in the light, and the rate at which this adjustment occurs initially will depend on changes in the relative signal strength from the two shoots. This signal must be linked to the carbohydrate productivity of each shoot to ensure efficient plant growth. It is the effect of the change in the signal strength that disproportionate allocation mimics quite crudely by ordering tillers in terms of their productivity. Once a difference in allocation between the two shoots has been established, the rate at which the less productive shoot gets removed from the system, depends both on the relative strengths of the resource signals and the potential shoot growth rate of the plant, because the latter affects the size of the deficit between resource supply and demand: the length of resource deficit periods increases with increased potential shoot growth rate. These extended periods of resource deficit further promote the inhibition of lateral buds, explaining tiller recruitment differences between species with faster and slower organ growth rates (Tomlinson & O'Connor 2005). In Chapter 9, changes to the shoot growth rate are simulated in order to explore the effects of this property on the growth of bunchgrass clones.

The growth behaviour demonstrated here arises from the demographic behaviour of tillers, ramets and ramet groups, which arises from the interaction between the architectural arrangement of bunchgrass clones and the nature of resource allocation (Herben & Suzuki 2002). The behaviour indicates that the population dynamics at the sub-clonal level have real effects that determine behaviour at the clonal level, validating the use of individual-based modelling techniques to assess growth at higher levels of organisation in plants (Judson 1994; Lafarge et al. 2005).

5 PROBLEM 2:   CLONAL INTEGRATION VERSUS NON-INTEGRATION IN BUNCHGRASS CLONES

Bunchgrass tufts usually consist of many disconnected ramet groups (Briske & Derner 1998). This non-integration can be explained on the basis of the developmental architecture of clones descended from a common parent (Wilhalm 1995): individual tillers have limited longevity and they die after flowering or they may senesce prematurely due to unfavourable environmental conditions. This in turn leads to the death of ramets, which breaks physiological connections between daughter ramets. These autonomous ramet groups (Tuomi & Vuorisalo 1989), form the base units that compete with one another for available resources within the same grass clone (Briske & Derner 1998). The relative intensities of intra-clonal and inter-clonal competition have been demonstrated to be comparable in several caespitose grasses (Briske & Butler 1989).

In the past, researchers focussed on the advantages of clonal integration, mainly equitable resource allocation across the clone, and assumed that clonal disintegration was disruptive (e.g. Alpert, Warembourg & Roy 1991). More recently, there has been a paradigm shift towards the advantages of physiological disintegration into smaller units (Kelly 1995) and it is apparent that these advantages must exceed the detrimental effects of competition among these smaller units (Briske & Derner 1998). This argument is based on the premise that clonal species are derived from an original obligately integrated progenitor (Kelly 1995).

The question is why would disintegration be advanatgeous? Previous hypotheses include the costs of maintaining vascular connections, the possibility of traumatic breakage, and escape of the genet from pathogen infestation (Kelly 1995). Both of the former hypotheses are irrelevant to bunchgrasses, which have closely spaced ramets, but the final hypothesis could have relevance (Briske & Derner 1998).

I propose that clonal non-integration in bunchgrasses may be related to improved temporal resource allocation efficiency across the clone. In Section 4 of this chapter it was demonstrated that growth in bunchgrasses shows strong temporal dependence between tillers maintained and ability to respond to shifts in environmental resource availability. It was demonstrated that bunchgrass clones that were more proportionate in resource allocation maintained more tillers but at the expense of individual growth. Although total growth of more proportionate clones was still greater than that achieved by more

disproportionate clones, growth efficiency (productivity per unit live shootmass) was reduced because less photosynthetically-productive tillers were maintained by resources supplied from more photosynthetically-productive tillers. This reduced the rate of regrowth after the flowering period because of the inefficient resource allocation. In both proportionate and disproportionate clones, clonal disintegration led to the death of less productive ramet groups as they competed with more productive ramet groups for limited available resources. Complete clonal integration could increase resource allocation inefficiency by forcing the clone to waste additional resources on unproductive ramet groups, thereby compromising its growth during resource-poor periods. This problem could outweight any benefits obtained by clonal integration during resource-rich periods.

To test this effect, I compare the growth of fully-integrated bunchgrass clones with non-integrated clones simulated with the model TILLERTREE, in an effort to determine whether or not non-integration is more beneficial than integration to the growth of bunchgrass clones.

5.1   Procedure

In the TILLERTREE model new ramet groups are formed when intermediate ramets die, which separates the live ramets on either side of the now-dead ramet into separate ramet groups. In order to observe what effect total integration has on the clone the rule that controls the formation of new ramet groups is inhibited. This means that although intermediate ramets may die on the clone, all live units remain connected and consequently share resources in every iteration.

Two simulations were run for clones with full integration, one with proportionate allocation ($A_\gamma = A_\beta = 1.00$) and the second with disproportionate allocation ($A_\gamma = A_\beta = 0.75$). These were compared to data for the non-integrated clones generated in the previous simulations.

5.2 Results

Both simulations with full clonal integration terminated prematurely, indicating that full integration was not sustainable. The proportionate clone terminated within four years while the disproportionate clone terminated in the thirteenth year. In this section I will only compare the effect of integration/ partial integration on the disproportionate clone.

Figure 8.6 shows live object numbers and the LAI for the disproportionate clone. These may be compared with Figures 8.1 and 8.2 which shows similar data for the disproportionate clone with non-integration arising from the splitting of ramet groups. Inter-annual variation in maximum live object number varies more greatly for the integrated clones than for the non-integrated clones. There is also much greater variation between the maximum live object number and minimum live object number on the integrated clone. The increased inter-annual variation in tiller production increased the variation in inter-annual live mass production (reflected in the LAI), and reduced the summed production over the years. This was associated with greater variation in live mass of individual organ types and the number of flowering tillers was substantially reduced every third year.

5.3 Discussion

The main effect of full clonal integration appears to be increased inter-annual variation in live object number, which in turn affects the productivity of the clone and even survival. During resource rich periods the integrated clone grows more quickly than the non-integrated clone. However during resource-poor periods the clone is forced to share resources between both productive and unproductive ramet groups, which compromosies individual performance and therefore total clonal growth during such periods. This causes large numbers of tillers to die over short periods, which reduces the clone's rate of regrowth because of the reduction in growth axes, and may even cause the entire clone to die. Non-integration provides a temporal benefit because more productive ramet groups do not have to share resources with less productive ramet groups, and therefore increase their ability to survive through resource-poor periods. Resource limitation during resource-poor periods kills less productive ramet groups, which provides a further benefit because removal of weak competitor ramet groups increases the resource space available to the survivors. This

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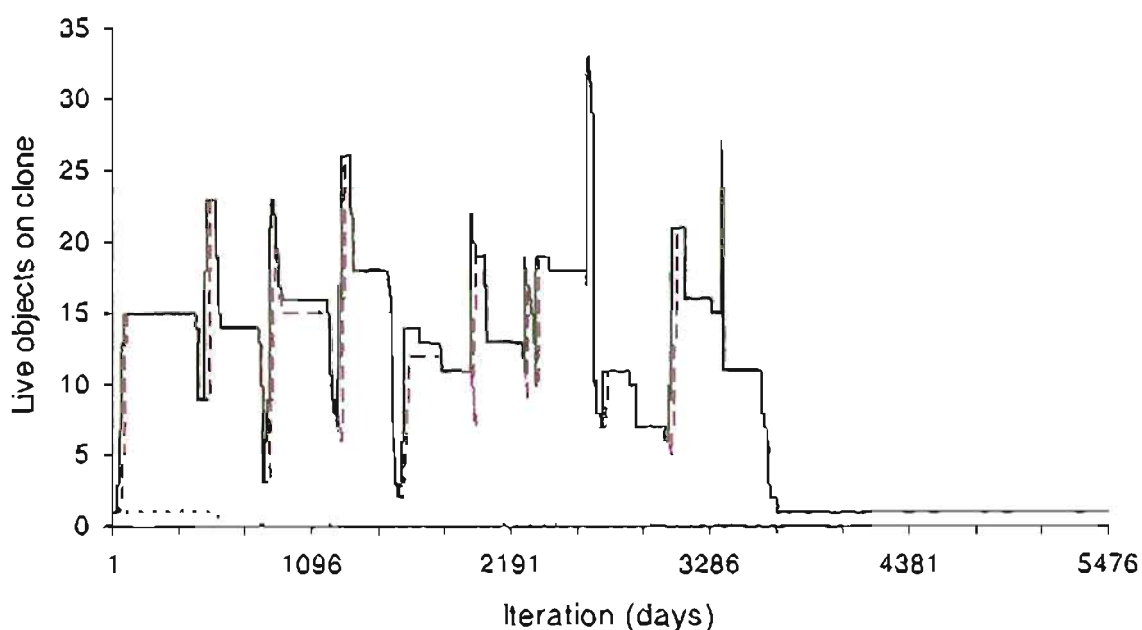
Figure 8.6a Number of live tillers (————), live ramets (— — —) and live ramet groups
(· · · · ·) recruited and surviving on a disproportionate clone ($A_\gamma = A_\beta = 0.75$) with full integration
across the clone. (Environmental conditions: Plant activity during the growing and non-growing
season as defined in Section 4.3 of Chapter 4. Growing season proceeds from Yearday 1 to
Yearday 242 of each year. Daily soil nitrogen availability as described in Section 3 of Chapter 4.)
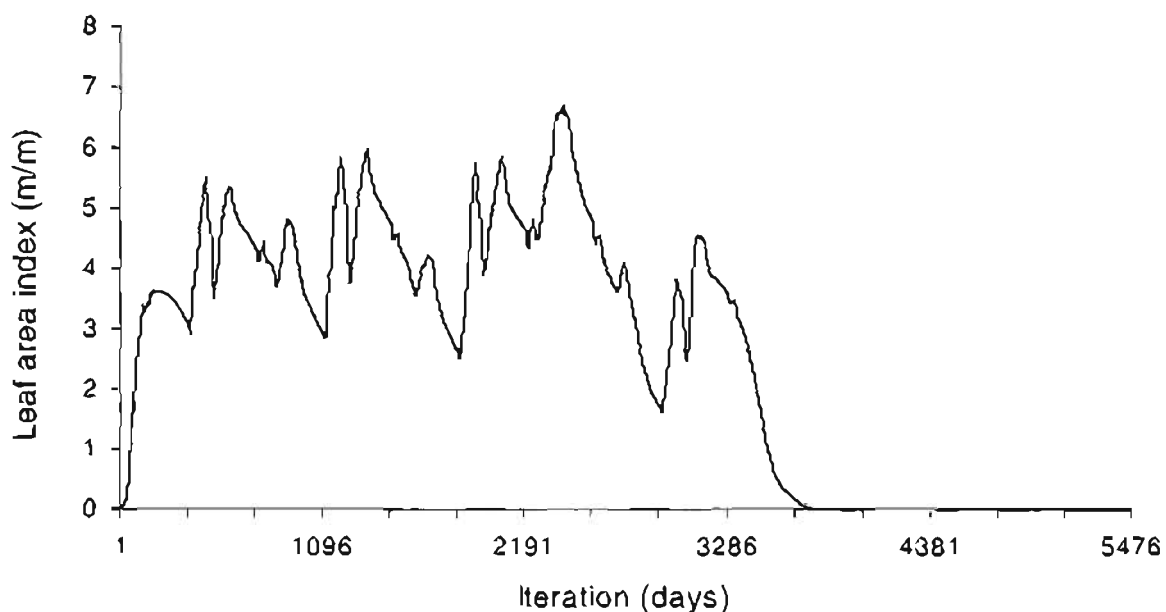
Figure 8.6b Leaf area index (LAI) at ground level of a disproportionate clone ($A_\gamma = A_\beta = 0.75$)
with full integration across the clone. (Environmental conditions: Plant activity during the growing
and non-growing season as defined in Section 4.3 of Chapter 4. Growing season proceeds from
Yearday 1 to Yearday 242 of each year. Daily soil nitrogen availability as described in Section 3 of
Chapter 4.)

is the process underlying the asymmetric competition among ramet groups that has been previously described (Tuomi & Vuorisalo 1989; Schwinning 1996).

In summary, non-integration in bunchgrass clones allows for more efficient and more stable growth than full clonal integration because it temporally pre-empts inefficient resource allocation during periods of resource restriction by reducing the number of objects sharing resources, which allows greater allocation to individuals, and improves their individual chances of overcoming resource restriction, and therefore improves the chances of clonal survival.

The benefit of non-integration to bunchgrass clones arises because of variability in daily growth potential caused by shifts in resource availability in humid grassland communities (Knapp et al. 1998). Growth in bunchgrass communities is co-limited by three main resources, namely light, water and nitrogen (Knapp et al. 1998). These resources are dynamically variable and plant growth in any season is not continuous or linear, but rather it expresses as a series of growth pulses in direct response to events influencing the relative availability of the three limiting resources. This means that growth is discontinuous and restricted in bunchgrass communities and subject to extended periods of resource insufficiency. In addition there are non-growing seasons each year when conditions are not conducive to growth, following which plants must regrow photosynthetic surfaces, often through closed canopies where light limitation is restrictive to regrowth (Chapter 7). Clonal non-integration favours survival of ramets on the largest ramet groups and avoids compromising their growth through resource wastage on less productive ramets, promoting rapid regrowth during resource-rich periods and resource conservation during resource-poor periods in the fitter ramet groups. Consequently clonal non-integration improves the efficiency of resource allocation that promotes survival and competitive ability of the clonal bunchgrass genet. This is a more plausible explanation for its evolution as a strategy than pathogen infestation as proposed by Kelly (1995).

It should be noted that this evidence for advantages of non-integration in bunchgrass clones does not invalidate the importance of clonal integration to other growth forms. Correlation between clonality in plant families found in Europe and resource gradients indicates that the strongest relationship exists between clonality and soil nutrient fertility (Groenendael et al. 1996). Consolidator strategists such as bunchgrasses are most abundant in nutrient–poor environments that are also dry and unshaded, providing corroborating evidence that non-integration in bunchgrasses improves resource capture and utilisation. By contrast spreading species are most abundant in nutrient-rich environments (Groenendael

et al. 1996). Worldwide stoloniferous grass species, which have well-developed spreading ramet connectors (Briske & Derner 1998), are abundant in grass communities where light is non-restrictive. The primary function of stoloniferous growth is spatial foraging for nutrients (Hutchings & de Kroon 1994), and maintaining large interconnected structures enables stoloniferous plants to supply enough resources for rapid spatial expansion into nutrient-rich patches (Evans 1992; Herben & Suzuki 2002).

Differences in clonal integration in plant growth forms may have evolutionary origins other than nutrient acquisition and competition. For instance, clonal integration in floating aquatics varies from strongly integrated, such as *Eichhornia crassipes* (Alpert *et al.* 1991), to weakly integrated, such as *Pistia stratiotes* (DeWald & Lounibos 1990). As both species occupy similar environments, this difference in growth strategy cannot be explained in terms of different responses to shifts in resource availability. Rather the explanation is structural: *Eichhornia crassipes* is an upright aquatic which easily falls over if grown individually, so the species forms strongly integrated mats to prevent this from happening. *Pistia stratiotes* has prostrate leaves without petioles and so cannot fall over. Therefore structural integration is unnecessary and non-integration promotes the species' invasive ability.

6   PROBLEM 3:   NECESSITY OF NITROGEN AND CARBOHYDRATE REQUIREMENTS FOR TILLER RECRUITMENT

There is sufficient evidence to indicate that secondary tiller recruitment is moderated by the nutritional status of the plant (Cline 1991). Current literature suggests that signals for both carbohydrate availability and nitrogen availability are necessary for tiller recruitment to occur (Tomlinson & O'Connor 2004). However there is much stronger empirical evidence for a link between nitrogen availability and tiller recruitment, than for carbohydrate availability and tiller recruitment. One explanation for this is that nitrogen is a much more limiting resource to bunchgrass growth over an entire season than carbohydrate simply because green leaves on bunchgrass plants need only pierce their own dead canopies to photosynthesise. Therefore the strong correlation between nitrogen and tiller recruitment, though certainly true, may be overshadow other requirements for recruitment (Tomlinson & O'Connor 2004).

In Section 1.1 of this chapter, a set of rules were defined that controlled tiller recruitment events in the TILLERTREE model. These included minimum concentrations of AVC and AVN after all existing growth requirements had been satisfied, in order to restrict tiller recruitment to resource-favourable conditions. The assumption made is that this strategy ensures appropriate tiller recruitment in response to the limiting resources light and soil nitrogen. However this strategy may reduce productivity because it is purely reactionary (if both AVC and AVN are in excess then additional growth may occur). An alternative strategy is that bunchgrasses may improve their ability to capture resources through a proactive strategy that is restricted by only one resource. In this strategy the bunchgrass plant could potentially pre-empt use of the second resource through 'speculative' recruitment based on the sufficiency of the first resource. Potentially this strategy would allow the clone to recruit more tillers for increased production when the second resource is available.

Based on the prevailing evidence it seems likely that nitrogen is the most critical requirement for secondary tiller recruitment. However for the purposes of this study I ignore this evidence in order to test what happens to simulated bunchgrass clones when they ignore either resource signal to direct tiller recruitment. In this section, the following question was asked: What are the consequences for clonal growth of dropping the AVC requirement or AVN requirement for tiller recruitment?

6.1   Procedure

The simulations were conducted using two resource allocation strategies, namely a proportionate strategy ($A_\gamma = A_\beta = 1.00$) and a disproportionate strategy ($A_\gamma = A_\beta = 0.75$), applied with either the AVC or AVN requirement for secondary tiller recruitment removed. These were compared to simulations for the two allocation strategies with both the AVC and AVN requirement included.

6.2   Results

6.2.1   Removing the AVC requirement for tiller recruitment

Removal of the AVC restriction on tiller recruitment increased tiller recruitment substantially each year across both proportionate and disproportionate clonal growth strategies. The increased tiller production was not sustainable on the proportionate clone, which terminated prematurely within three years of initiation (Figure 8.7). This was because the proportionate strategy does not discriminate among objects, which caused a far larger set of live tillers to be kept alive at any one time than the disproportionate strategy. This meant that the amount of carbohydrate and nitrogen available to individual tillers for spring regrowth was diluted even further, so there was insufficient growth on individual tillers to overcome the spring resource bottleneck.

The removal of the AVC restriction on tiller recruitment similarly increased tiller recruitment on the disproportionate clone (Figure 8.8), but reduced nitrogen absorption and net photosynthesis (Figure 8.9). The effect is related to the overproduction of tillers during the post-flowering period which reduces the efficiency with which resources are allocated. A large number of these smaller tillers survive through winter but die in early spring, which reduces the ability of the clone to accumulate soil nitrogen when it is available. This can also be seen by the distribution of live root mass and live shoot mass across the clone, which indicates that the root-to-shoot ratio is less skewed in favour of shoots in the post-flowering period (Figure 8.9). This is because reduced plant material accumulates in the canopy due to the reduced clonal growth. Improved light efficiency in the canopy means that photosynthetic efficiency is greater in the post-flowering period.

Figure 8.7   Effect of removing the AVC tiller recruitment restriction rule on the live structures maintained by the proportionate allocation clone (——— live tillers, — — — live ramets, ······ live ramet groups). Note the premature termination during the third growing season. (Environmental conditions: Plant activity during the growing and non-growing season as defined in Section 4.3 of Chapter 4. Growing season proceeds from Yearday 1 to Yearday 242 of each year. Daily soil nitrogen availability as described in Section 3 of Chapter 4.)

Figure 8.8 Effect of the AVC tiller recruitment restriction rule on the live structures maintained by the disproportionate allocation clone ($A_\gamma = 0.75$, $A_\beta = 0.75$) (——— live tillers, — — — live ramets, · · · · · live ramet groups). a. With AVC rule, b. No AVC rule. (Environmental conditions: Plant activity during the growing and non-growing season as defined in Section 4.3 of Chapter 4. Growing season proceeds from Yearday 1 to Yearday 242 of each year. Daily soil nitrogen availability as described in Section 3 of Chapter 4.)
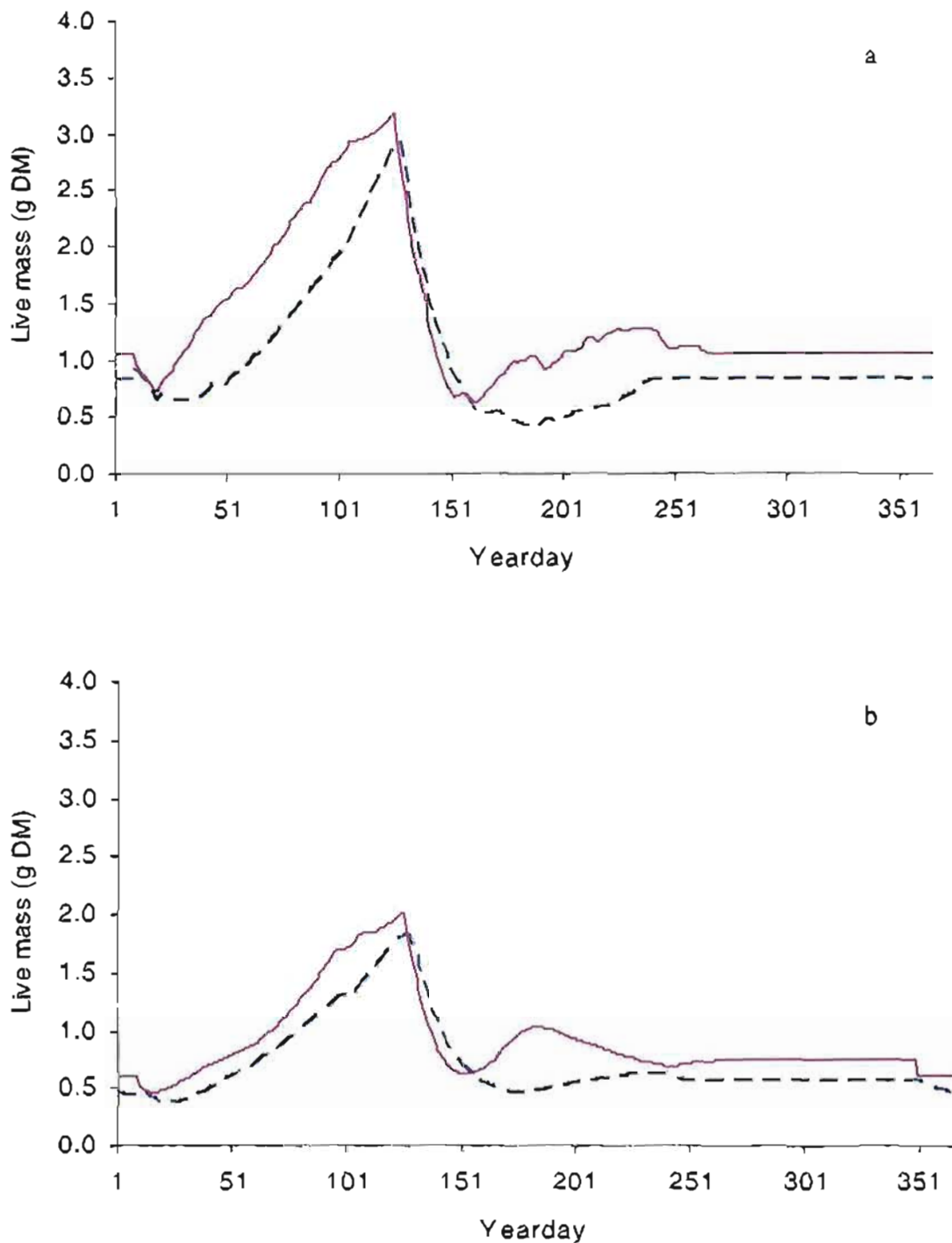
Figure 8.9   Effect of the AVC tiller recruitment restriction rule on average daily live shoot mass (———) and live root mass (— — —) maintained by the disproportionate allocation clone (A_γ = 0.75, A_β = 0.75). a. With AVC rule, b. No AVC rule. (Environmental conditions: Plant activity during the growing and non-growing season as defined in Section 4.3 of Chapter 4. Growing season proceeds from Yearday 1 to Yearday 242 of each year. Daily soil nitrogen availability as described in Section 3 of Chapter 4.)

6.2.2 Removing the AVN requirement for tiller recruitment

Removing the AVN requirement caused all the simulations to terminate prematurely, although the disproportionate clone survived for longer than the proportionate clone (Figure 8.10). The growth was characterised by very large amounts of tiller recruitment each year followed by large amounts of tiller dieback. Individual tillers grew very poorly so biomass accumulation was substantially reduced. This indicates that limits on nitrogen were overriding over limits on photosynthetic potential.

Table 8.2   Effect of removing resource requirements for tiller recruitment on average annual resource capture by clones

Recruitment Rule	N absorption (g N)				Net Photosynthesis (g CHO)			
	Proportionate		Disproportionate		Proportionate		Disproportionate	
	$A_\gamma = 1.00, A_\beta = 1.00$		$A_\gamma = 0.75, A_\beta = 0.75$		$A_\gamma = 1.00, A_\beta = 1.00$		$A_\gamma = 0.75, A_\beta = 0.75$	
	Mean	S.E.	Mean	S.E.	Mean	S.E.	Mean	S.E.
AVC and AVN requirements	0.124	0.001	0.101	0.001	21.789	0.354	19.337	0.159
AVN requirement only	-	-	0.070	0.005	-	-	14.258	0.673
AVC requirement only	-	-	-	-	-	-	-	-

6.3   Discussion

Removing the AVC requirement for tiller recruitment reduced productivity on the disproportionate clone and terminated growth on the proportionate clone. Removing the AVC requirement increased tiller recruitment which reduced the temporal efficiency of resource allocation because limited nitrogen resources were wasted on the additional recruited tillers. The disproportionate strategy clone survived insensitivity to internal carbohydrate availability because nitrogen limitations kept tiller recruitment in check.

Insensitivity of the tiller recruitment rules to nitrogen availability was always catastrophic to clonal growth, because this caused the clone to recruit far too many tillers
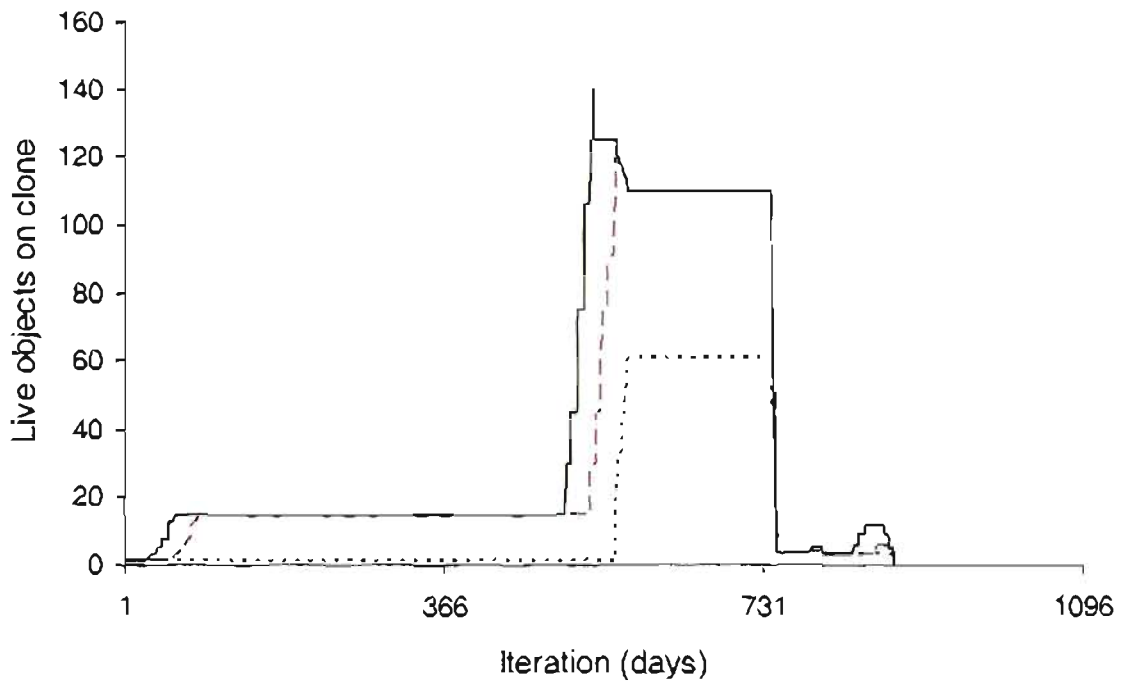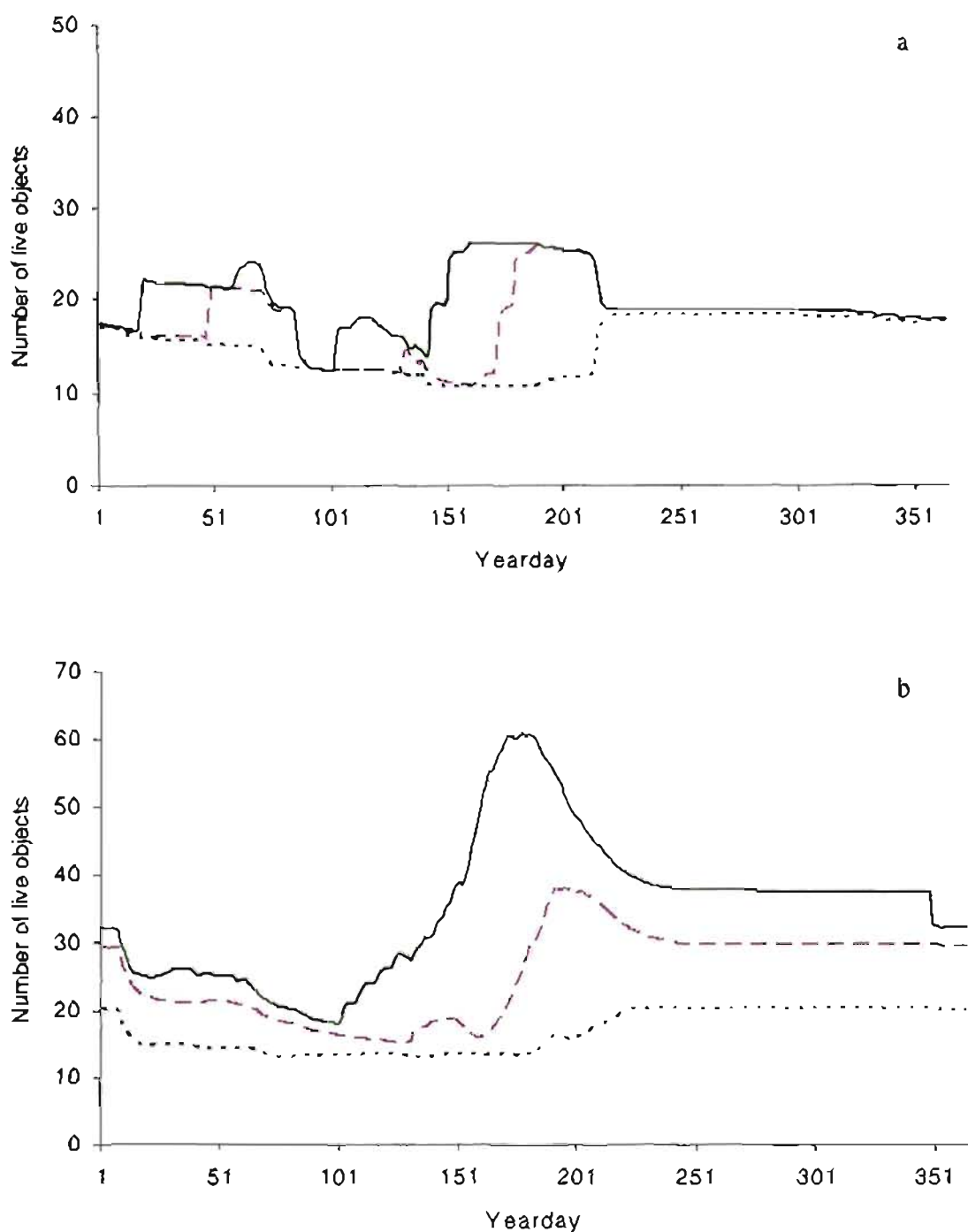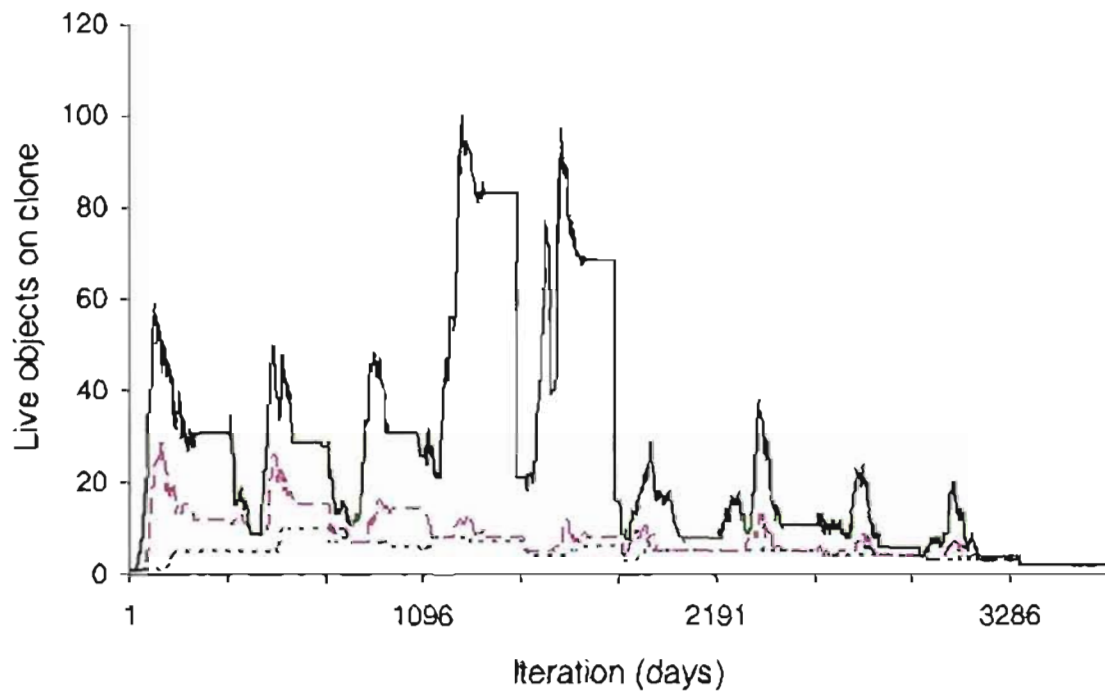
Figure 8.10 Effect of removing the AVN tiller recruitment restriction rule on the live structures maintained by the disproportionate allocation clone (——— live tillers, — — — live ramets, ······ live ramet groups). Note the premature termination during the ninth growing season. (Environmental conditions: Plant activity during the growing and non-growing season as defined in Section 4.3 of Chapter 4. Growing season proceeds from Yearday 1 to Yearday 242 of each year. Daily soil nitrogen availability as described in Section 3 of Chapter 4.)

for the available resource space, which increased the resource wastage on the additional recruited tillers. This indicates that limits on nitrogen availability were overriding over limits on photosynthetic ability.

The simulation evidence presented here provides support for the assertion that tiller recruitment, at least in bunchgrasses, is controlled by signals for both nitrogen availability and carbohydrate availability, because these reflect the availability of environmental resources (Tomlinson & O'Connor 2004). The evidence suggests that tiller recruitment responds to nitrogen availability simply because it is the most limiting resource while it responds to carbohydrate availability because this improves resource allocation efficiency by reducing resource wastage on non-sustainable structures. No benefit is gained by ignoring either resource, because both resources are sufficiently limiting to growth of bunchgrass clones.

Possibly the strategy of secondary resource 'pre-emption', which bases tiller recruitment on signals of one resource only, may be very effective in environments where growth is substantially more restricted by that one resource over all others. For exmaple rafting aquatics such as *Eichornnia crassipes* (Alpert *et al.* 1991) and stoloniferous grasses (Hutchings & de Kroon 1994) are not usually limited by light, so dependence of tiller recruitment on a light signal would probably be unnecessary. Therefore growth may respond to nitrogen limitation only. Lateral shoot outgrowth in species growing in permanently shaded environments (e.g. understorey herbs) is insensitive to the light signal (Bain & Attridge 1988; Dudley & Schmitt 1995). This probably occurs because irradiance does not vary greatly in these environments, so no benefit is gained from responding to shifts in irradiance or light quality (Morgan & Smith 1979). Shade-grown species are physiologically adapted to maximise photosynthetic efficiency in the poor light environments they inhabit and structurally adapted to cope with low carbohydrate production (see Givnish 1988).

Shade-plant insensitivity to light signals, potential light-insensitivity of stoloniferous species abundant in environments where light is non-limiting, and dual requirement for nitrogen and light for growth efficiency and productivity in bunchgrasses demonstrated here, together provide the basis for a hypothesis on the nutrient requirements of plants for tiller recruitment: tiller recruitment is adapted to cope with temporal resource variability in any given environment. Consequently tiller recruitment responds only to resources which are both limiting to growth and temporally variable because those resources determine daily growth potential in any given environment.

141

7   CONCLUSIONS

The simulations conducted here indicate that there is some overlap between the behaviour generated by different properties of clonal bunchgrasses. Specifically, when these properties promote increased tiller numbers on individual ramet groups, be this through increased tiller recruitment, more proportionate resource allocation or clonal integration, the clonal behaviour tends to become less stable and fluctuation increases relative to behaviour generated on clones that promote smaller tiller numbers on individual ramet groups. The reason for this is that increased tiller number on individual ramet groups increases the growth potential of those ramet groups during periods when environmental resources are abundant, but it also increases resource wastage during periods when environmental resources are restrictive as more sinks must be maintained, which in turn may increase the risk of death. All this evidence suggests that at least with respect to clonal plants there is a trade-off in growth strategy which forces clonal plants to follow either rapidly-growing, but short-lived life strategies (annuals, biennials) or slower-growing, long-lived life strategies (perennials). These properties appear to be similar to those possessed by r- and K-strategists respectively (MacArthur & Wilson 1967). The trade-off is induced by the dynamic nature of environmental resource availability in bunchgrass communities (Knapp *et al.* 1998), which rapidly changes the growth potential of bunchgrass clones.

Chapter 9:

Trade-off in Clonal Bunchgrasses between Ability to Capture Nitrogen and Ability to Compete for Light

Growth in humid grasslands is controlled by the alternate limitation of three resources, namely light, nitrogen and water (Knapp *et al* 1998). Nitrogen is the most limiting environmental nutrient to plant growth because its availability is tied both to wetting and drying cycles and the growth and death of soil microbes and plants that compete for the resource (Birch 1958). Light is limited to tufted grasses because of the manner in which they grow: shoots expand from meristems usually located close to the ground surface, which causes a large amount of biomass to accumulate close to the soil surface. This reduces light penetration and consequently restricts photosynthetic production. Soil water pressure determines periods of growth and no-growth in plants, as plants depend on moisture to transpire. Water use may also distinguish species because some are able to continue growth at much lower soil water pressures than others, as wilting point is a species-specific trait (Penning de Vries *et al.* 1989).

There is evidence that species are distributed differentially along nitrogen and light gradients (Tilman & Wedin 1991), suggesting that some species are better competitors for nitrogen and others are better competitors for light. This has provided the basis for the hypothesis that competitive advantage could be determined by an enforced trade-off between the ability to capture carbon and the ability to capture and retain nitrogen in low-resource environments (Tilman 1988). Tilman & Wedin (1993) found that slow-growing plants were able to reduce soil nitrogen concentration to lower levels than their competitors, suggesting that they are better able to utilise the available nitrogen. However the view that this effect is due to a superior ability to extract nitrogen from the soil at low concentrations (Tilman 1988) has been questioned (Grime 2001). An alternative hypothesis proposes that competitive rankings should remain the same across productivity gradients (Grime 1979), and suggests that the nutrient gradient effect on species composition may be due to additional environmental factors such as differential herbivory that disadvantages faster-growing species more than slower-growing species (Grime 2001). A recent study that considered competitive growth of five perennial C_4 bunchgrass species in response to

different levels of fertility, irrigation and defoliation frequency (Fynn, Morris & Kirkman 2005b), demonstrated that certain species changed dominance along fertility gradients in the no-defoliation treatments while a different species (*Themeda triandra*) became dominant in all the defoliation treatments regardless of fertility. This provides evidence for the trade-off hypothesis of Tilman (1988), and further suggests two trade-off axes, namely a trade-off between ability to compete in nutrient-rich and nutrient-poor environments and a second trade-off between ability to compete in regularly defoliated versus non-defoliated environments. In this chapter I ignore defoliation effects, and focus on providing a mechanism for competitive trade-offs in bunchgrasses between ability to capture nitrogen and ability to compete for light.

Species in nitrogen-poor environments often have slower relative growth rates than species in nitrogen-rich environments (Grime & Hunt 1975). Chapin (1980) suggested that under nutrient limitation slow-growing species "function closer to their optimal growth and metabolic rate and may therefore be more fit in a low-nutrient environment than a rapidly-growing species". However inherently fast-growing species still have equal or higher relative growth rates than inherently slow-growing species when grown at low nutrient availability (Berendse & Elberse 1989, Van der Werf *et al.* 1993a). Assuming that herbivory is not involved, the question then is why these fast-growing species do not also dominate low nutrient environments under natural conditions?

On the basis of the hypothesis posed by Chapin (1980), Van der Werf *et al.* (1993b) designed a model to test whether plants growing in nutrient-poor environments utilise nitrogen better with respect to their optimum growth rates than species of nutrient-rich environments. Their model found no difference in productivity between the plant types at low nutrient availability and concluded that optimal partitioning could not explain the success of slow-growing species in nutrient-poor environments. They suggested that the success must be based on other plant characteristics selected for poor nutrient environments such as slow biomass turnover rates which reduce nitrogen-loss rates. This explanation may be plausible for plants from different growth forms, but it is unlikely explain shifts in bunchgrass species composition in response to different non-selective defoliation treatments (Everson & Tainton 1984; Fynn *et al.* 2005a) because of the short longevity of bunchgrass ramets (Briske & Derner 1998).

Most researchers agree that competition on nutrient poor soils relates primarily to nitrogen accumulation and conservation, and secondly to phosphorous accumulation and conservation. One important criticism of the high-nutrient, low-nutrient competition studies

conducted by most researchers is that they compare growth of inherently-fast and inherently-slow growing species under continuously-high and continuously-low nutrient environments (Grime 2001). This does not match natural conditions where nitrogen and other minerals become available in pulses. Results from one experiment designed to test the effect of pulsed nutrient supply to fast-growing *Arrhenatherum elatius* and slow-growing *Festuca ovina* plants (Campbell & Grime 1989) suggested that the inherently-fast growing species lost their competitive advantage when minerals nutrients were fed in pulses. The authors concluded that the results were consistent with the differences in the mechanisms of resource foraging predicted by the C-S-R model (Grime 1979) in that the slower species maintained more root biomass under conditions of stress and was therefore better able to utilise resource pulses. The results certainly suggest that there is some trade-off between ability to compete for light and ability to compete for nitrogen. The question is what differences in growth between the fast-growing and slow-growing species could explain this behaviour?

Many models designed to consider competitive differences between species (including Van der Werf *et al.* 1993b) are not structurally-explicit, and rather only recognise the growth of amorphous biomass partitioned into a number of categories, usually organ types. Therefore they do not consider the discrete tiller architecture that characterises the growth of bunchgrasses, and are unable to consider the effects of organ distribution explicitly. The discrete behaviour of tiller recruitment may substantially alter seasonal distributions in productivity. Critically the rate at which a bunchgrass clone can grow (biomass per unit time) depends both on the number of tillers and the growth rates of their perennating organs. This means that plants with more live tillers with slower organ growth rates could grow more quickly than plants with faster organ growth rates but fewer live tillers.

The population dynamics of clonal plants given above suggest that a key problem that may have limited the debate on competitive ability of different plants may be the lack of a clear, mechanistic definition of 'inherently faster-growing' plants versus 'inherently slower-growing' plants. Therefore 'inherently faster-growing' plants are defined here as plants with potentially faster individual organ growth rates. Under non-limiting or constant resource conditions, it is likely that clones of these plants with relatively faster-growing organs may grow more quickly than clones of species with relatively slower-growing tillers. Under non-constant and limiting resource conditions this result may not necessarily be true, because resource competition among connected shoots and resultant population dynamics of

those shoots may change the number of live shoots maintained over resource-poor periods, which limits the total regrowth potential of the plant.

The ability to recruit tillers rapidly during periods of high nitrogen availability would allow a bunchgrass clone to grow rapidly in response to periods of high nitrogen availability and thereby improve its ability to utilise the nutrient pulse. There is sufficient evidence to suggest that tiller recruitment is restricted by plant nutrition status (Tomlinson & O'Connor 2004). The Nutrition Hypothesis of control over lateral bud outgrowth (the process by which secondary tillers are recruited; see Appendix A2) is determined by periods of resource excess in plants (see Cline 1991), which in turn is determined by the balance between resource sink demand and source supply rates. In a previous paper we found that tiller recruitment in spring was inversely related to organ extension rate on bunchgrass species growing in the Southern Tall Grassveld (Tomlinson & O'Connor 2005). The reason for this may be that plants with larger individual organ growth rates have fewer tiller recruitment opportunities because their daily resource demands keep excess resource concentrations below levels required for secondary tiller recruitment. This means that species with faster organ growth rates may have lower tiller recruitment rates, and therefore could be slower in responding to nutrient pulses than species with slower organ growth rates but higher tiller recruitment rates, because total plant growth rate is limited by the number of growth axes.

Shifts in bunchgrass species composition in response to non-selective defoliation regimes that create different light environments in the humid grasslands of South Africa (Everson & Tainton 1984; Fynn et al. 2005a) have beeen associated with two important tiller traits that are positively correlated with one another: blade extension rate and blade maximum potential length (Tomlinson & O'Connor 2005). The taller and faster-growing species Eragrostis curvula is more dominant on less-frequently defoliated treatments, where light penetration is reduced by the buildup of plant dry matter in the canopy, while the shorter and slower-growing species Themeda triandra is associated with frequently defoliated treatments where light is less restrictive to growth (Fynn et al. 2005a; Tomlinson & O'Connor 2005). Therefore either or both tiller daily growth rate and tiller height may influence the ability of individual bunchgrass species to acquire and utilise light and soil nutrient resources.

A further factor which may contribute to this problem is disproportionate allocation of resources among live shoot objects. In Chapter 8, the effects of disproportionate allocation of resources among connected live objects on a plant were explored. It was

146

shown that disproportionate allocation across live objects provides grass clones with a number of benefits, which arose from the promotion of photosynthetically more productive tillers at the expense of photosynthetically less productive tillers. Disproportionate allocation passively removed less efficient tillers, which reduced the number of tillers drawing resources during periods of low environmental resource availability and therefore increased stability. However this was a trade-off because increased tiller mortality reduced the number of live tillers that survived at any one time, which meant that plant growth in response to nutrient resource periods was more restricted on disproportionate clones than on proportionate clones because of the limit on growth axes. Increasing daily growth rates could increases the rate at which disproportionate allocation removes less productive tillers, increasing reduction of growth axes during resource-poor periods and consequently slowing regrowth on species with faster individual tiller growth rates.

In this chapter I use the TILLERTREE model to test the consequences of different leaf growth rates and leaf potential lengths on tiller recruitment and survival, resource capture and biomass production of individual clonal bunchgrass genets, in order to determine whether changes to these simple parameters leads to trade-offs between the ability to compete for light and the ability to compete for soil nitrogen. In doing this I assume that the Nutrition Hypothesis of tiller recruitment is valid based on the accumulated evidence on tiller recruitment (Tomlinson & O'Connor 2004).

The following questions were asked:

1. How do changes in the leaf mass growth rate affect tiller population size, resource capture and productivity of clonal genets?

2. How do changes in the leaf potential length affect tiller population size, resource capture and productivity of clonal genets?

1 METHODS

Across bunchgrass species, leaf extension rate is often positively correlated with leaf maximum potential length, and the species may have substantially different leaf mass-to-length ratios (Appendix A1). Consequently daily leaf resource demand is equal to the product of extension rate and mass gain rate per unit length. Therefore it is necessary to

147

distinguish the effects of leaf daily extension rate, leaf daily mass gain rate, and leaf potential length.

In order to distinguish the effects of leaf daily mass growth rate and leaf potential length, only the extension growth rates, mass gain rates and potential lengths of leaves (blades and sheaths) were manipulated on the existing *Themeda triandra* clone. Simulations were run in which the chosen parameters were changed by 50%, 100%, 150% and 200% respectively. Importantly the changes were applied in such a way that they did not change the rate at which leaves were recruited and therefore did not change the seasonal timing of growth events, such as flowering. This was necessary because nitrogen availability was seasonal, so changes in the seasonal distribution of growth processes would have confounded the behaviour of clones.

Three sets of simulations were conducted to distinguish the effects of leaf daily mass growth rate and potential leaf length, using the parameters maximum leaf extension rate, maximum potential leaf length and leaf mass-to-length ratio. These were as follows:

1. Tillers that range from short-and-light to tall-and-heavy

Both maximum leaf extension rate and maximum potential leaf length were changed together, so that they were 50%, 100%, 150% and 200% respectively of the original value. This created four clones with tillers that ranged from short, light and slow-growing, through to tall, heavy and fast-growing. Therefore their leaf daily mass growth rates were 50%, 100%, 150% and 200% of the original clonal tiller respectively.

2. Tillers with the same height but different leaf thickness

All four clones had the same maximum potential leaf lengths, but different mass-to-length ratios that were 50%, 100%, 150% and 200% of the original value. Therefore their daily leaf mass growth rates were 50%, 100%, 150% and 200% of the original clonal tiller respectively.

3. Tillers that range from short-and-fat to tall-and-thin

Both maximum leaf extension rate and maximum potential leaf length were changed together by 50%, 100%, 150% and 200% respectively, while leaf mass-to-length ratio was changed in the inverse way by 200%, 100%, 67.66% and 50%. This ensured that leaf daily mass growth rates were identical across the four clones, but partitioned differently in vertical space.

In all simulations, it was assumed that there was disproportionate allocation across shoot objects on the basis of photosynthetic productivity (A_γ = 0.75, A_β = 0.75).

Growth of each clone was simulated for 10 000 day iterations with no defoliation in order to determine the average annual growth behaviour and productivity. All simulations survived for the entire 10 000 iterations. Two types of data were considered for the analysis: the long-term average annual behaviour and productivity was calculated from data for the 6th to 27th years, and initial growth was recorded for the first five years after initiation. The long-term average annual data provided information on the seasonal growth patterns of the clones and how they responded to the seasonality of resource availability. The initial growth provided information on how quickly each clone occupied the available resource space and the manner by which this resource occupation was achieved.

2 RESULTS

2.1 Tillers that range from short-and-light to tall-and-heavy

2.1.1 Average annual behaviour

Table 9.1 shows summarised data for the four clones grown with different leaf extension rates and associated maximum potential leaf lengths, but identical mass-to-length ratios. Average annual productivity, as measured by annual summed growth, annual net photosynthesis and annual nitrogen absorption was highest on the clone with slowest extension rate and shortest leaves and decreased with increasing tiller size and leaf growth rate.

Maximum annual organ mass values varied across the clones because these were maxima for the entire season of growth. Leaf mass (blade mass and sheath mass) was lowest on the clone with shortest tillers, and highest on the clone with second shortest tillers, indicating that it was not correlated with leaf extension rate and potential leaf length. Internode mass and flower mass, were largest on the clone with slowest leaf extension and shortest tillers, and decreased with increasing extension rate and increasing potential leaf length. These two properties are associated with number of flowering tillers, which was highest on the clone with slowest extension rate and shortest tillers and decreased with increasing leaf extension rate and increasing potential leaf length.

149

Table 9.1 Average annual performance of modelled clones of *Themeda triandra* with different leaf extension rates and leaf maximum potential lengths, but the same mass-to-length ratio. Tillers range from potentially short-and-light to potentially tall-and-heavy.

	Allocation procedure							
	Short-and-light						Tall-and-heavy	
Leaf extension rate	x0.5		x1.0		x1.5		x2.0	
Potential leaf length	x0.5		x1.0		x1.5		x2.0	
Mass-to-length ratio	x1.0		x1.0		x1.0		x1.0	
	Mean	S.E.	Mean	S.E.	Mean	S.E.	Mean	S.E.
Average reproductive tiller data								
Number of flowering tillers	9.59	0.51	7.09	0.020	5.77	0.22	6.64	0.14
Maximum blade mass (g tiller^{-1})	0.064	0.001	0.126	0.003	0.150	0.003	0.149	0.002
Maximum sheath mass (g tiller^{-1})	0.022	0.001	0.043	0.001	0.050	0.001	0.047	0.001
Max internode mass (g tiller^{-1})	0.197	0.007	0.214	0.005	0.199	0.006	0.152	0.002
Maximum flower mass (g tiller^{-1})	0.034	0.001	0.041	0.001	0.042	0.001	0.038	0.001
Maximum culm length (mm)	522.47	16.77	564.07	12.41	502.88	11.09	409.17	5.36
Average clonal organ mass								
Maximum blade mass (g)	0.829	0.027	1.082	0.021	1.039	0.025	1.127	0.011
Maximum sheath mass (g)	0.268	0.006	0.336	0.005	0.319	0.006	0.339	0.003
Maximum internode mass (g)	1.892	0.071	1.512	0.018	1.140	0.025	1.007	0.009
Maximum flower mass (g)	0.314	0.012	0.285	0.004	0.239	0.005	0.251	0.003
Average clonal annual production								
Net photosynthesis (g CHO)	20.977	0.340	19.337	0.159	17.233	0.264	16.932	0.102
N absorption (g N)	0.117	0.002	0.101	0.001	0.093	0.001	0.089	0.001
Summed growth (g CHO)	14.999	0.243	13.683	0.094	12.517	0.196	12.281	0.068
Summed growth deficit (g CHO)	121.636	4.030	122.242	2.014	106.565	2.955	98.003	2.064

Live object number

The average live number of objects on each clone each day in a year is given in Figure 9.1. The number of live objects maintained across a year on each clone was highest on the clone with slowest leaf growth rate and smallest tillers, and decreased with increasing tiller size.

The seasonal tiller recruitment patterns were similar across all clones with two tiller recruitment periods, the first during early spring and a second, larger recruitment during the post-flowering period. Absolute recruitment on the slowest leaf extension clone was greater than on the other clones, but the relative size of the tiller recruitment (tillers recruited per parent tiller) during the post-flowering period was similar across the clones.

The clone with smallest tillers and slowest extension rate also showed distinctly different behaviour from the other clones in that the ramet groups on average consisted of more than one ramet at all times of the year, whereas the other clones always reduced to ramet groups consisting of one ramet and one tiller during the non-growing period.

Live clonal mass and daily resource capture

The average live root and live shoot mass on each clone each day in a year is given in Figure 9.2. Daily clone net photosynthesis and soil nitrogen absorption are presented in Figure 9.3.

Live clonal shoot mass and root mass over winter was greatest on the clone with smallest tillers and slowest leaf extension rate and decreased with increasing extension rate. Live clonal mass was positively associated with live tiller number. The reason for this is that internode mass does not die over winter. Therefore clones with more tillers had more live internode mass, which caused them to maintain more live biomass over winter than clones with fewer tillers. The combined greater live root biomass and live tiller number allowed the clone with smallest tillers and slowest leaf extension rate to accumulate more nitrogen each year through greater nitrogen capture at the start of spring regrowth than any of the other clones. Nitrogen capture decreased with decreasing pre-spring biomass, and consequently decreased through the clones as leaf extension rate and tiller size increased. Clones with faster extension rates overcome photosynthetic limitation in early spring more quickly. This is corroborated by the fact that average annual clonal root-to-shoot ratio
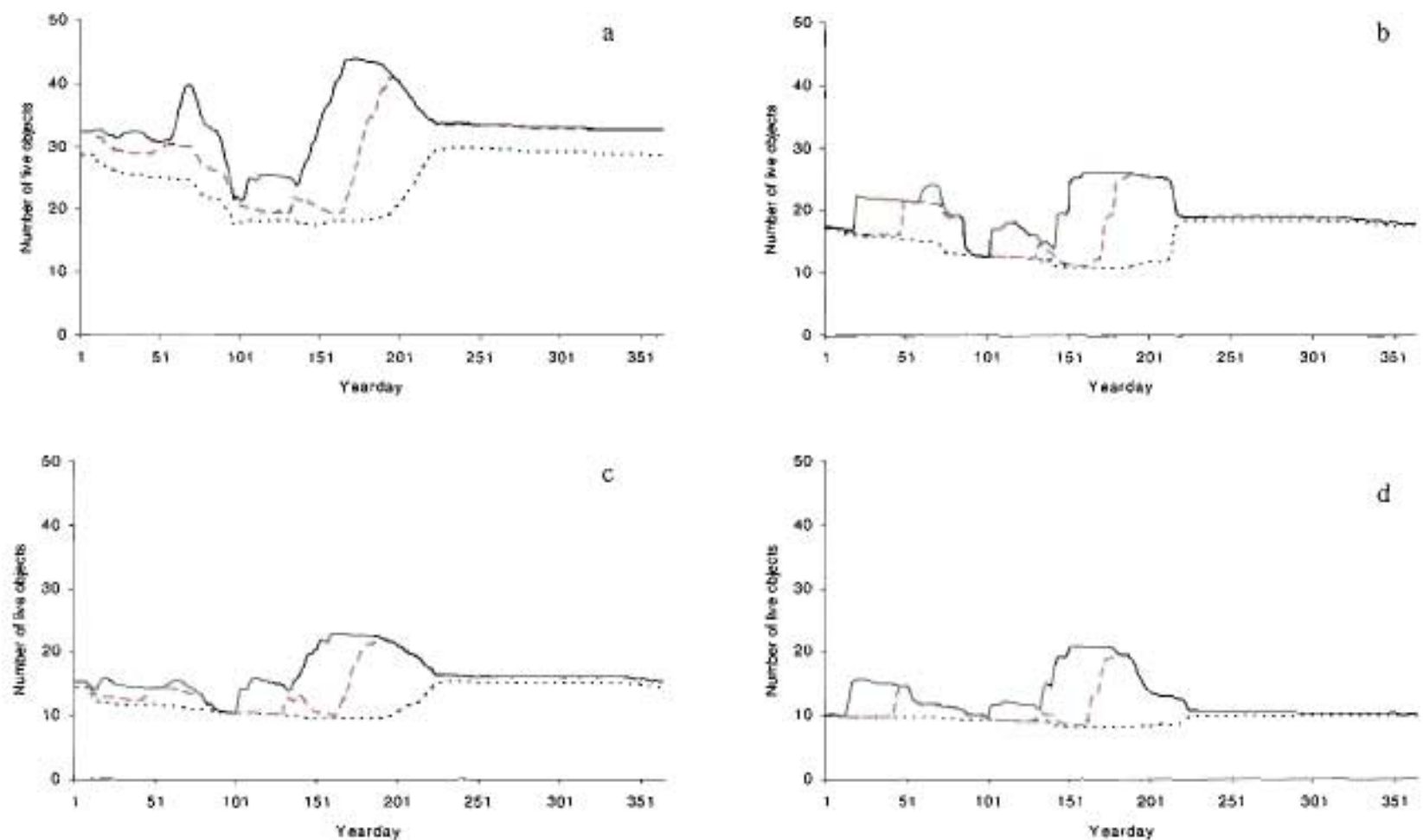
Figure 9.1 Average clonal daily number of live tillers (——), live ramets (– – –) and live ramet groups (········) on four clones of the modelled grass *Themeda triandra* with different leaf extension rates and maximum potential leaf lengths, but identical leaf mass to length ratios. a. Leaf extension rate x0.5, maximum potential length x0.5; b Leaf extension rate x1.0, maximum potential length x1.0; c. Leaf extension rate x1.5, maximum potential length x1.5; d. Leaf extension rate x2.0, maximum potential length x2.0. (Assumptions: Two blades remain alive over winter to ensure spring regrowth. Disproportionate allocation: $A_\gamma = 0.75$, $A_\beta = 0.75$.) (Environmental conditions: Plant activity during the growing and non-growing season as defined in Section 4.3 of Chapter 4. Growing season proceeds from Yearday 1 to Yearday 242 of each year. Daily soil nitrogen availability as described in Section 3 of Chapter 4.) (Environmental conditions: Plant activity during the growing and non-growing season as defined in Section 4.3 of Chapter 4. Growing season proceeds from Yearday 1 to Yearday 242 of each year. Daily soil nitrogen availability as described in Section 3 of Chapter 4.)

Figure 9.2   Average daily live shoot mass (————) and live root mass (— — —) on four clones of the modelled grass *Themeda triandra* with different leaf extension rates and maximum potential leaf lengths, but identical leaf mass to length ratios. a. Leaf extension rate x0.5, maximum potential length x0.5; b Leaf extension rate x1.0, maximum potential length x1.0; c. Leaf extension rate x1.5, maximum potential length x1.5; d. Leaf extension rate x2.0, maximum potential length x2.0. (Assumptions: Two blades remain alive over winter to ensure spring regrowth. Disproportionate allocation: $A_\gamma = 0.75$, $A_\beta = 0.75$.)   (Environmental conditions: Plant activity during the growing and non-growing season as defined in Section 4.3 of Chapter 4. Growing season proceeds from Yearday 1 to Yearday 242 of each year. Daily soil nitrogen availability as described in Section 3 of Chapter 4.)

Figure 9.3   Average daily net photosynthetic production (a) and soil N absorption (b) on four clones of the modelled grass *Themeda triandra* with different leaf extension rates and maximum potential leaf lengths, but identical leaf mass to length ratios. (——— Leaf extension rate x0.5, maximum potential length x0.5; — — — Leaf extension rate x1.0, maximum potential length x1.0; — · — Leaf extension rate x1.5, maximum potential length x1.5; ········ Leaf extension rate x2.0, maximum potential length x2.0.) (Assumptions: Two blades remain alive over winter to ensure spring regrowth. Disproportionate allocation: $A_\gamma = 0.75$, $A_\beta = 0.75$.) (Environmental conditions: Plant activity during the growing and non-growing season as defined in Section 4.3 of Chapter 4. Growing season proceeds from Yearday 1 to Yearday 242 of each year. Daily soil nitrogen availability as described in Section 3 of Chapter 4.)
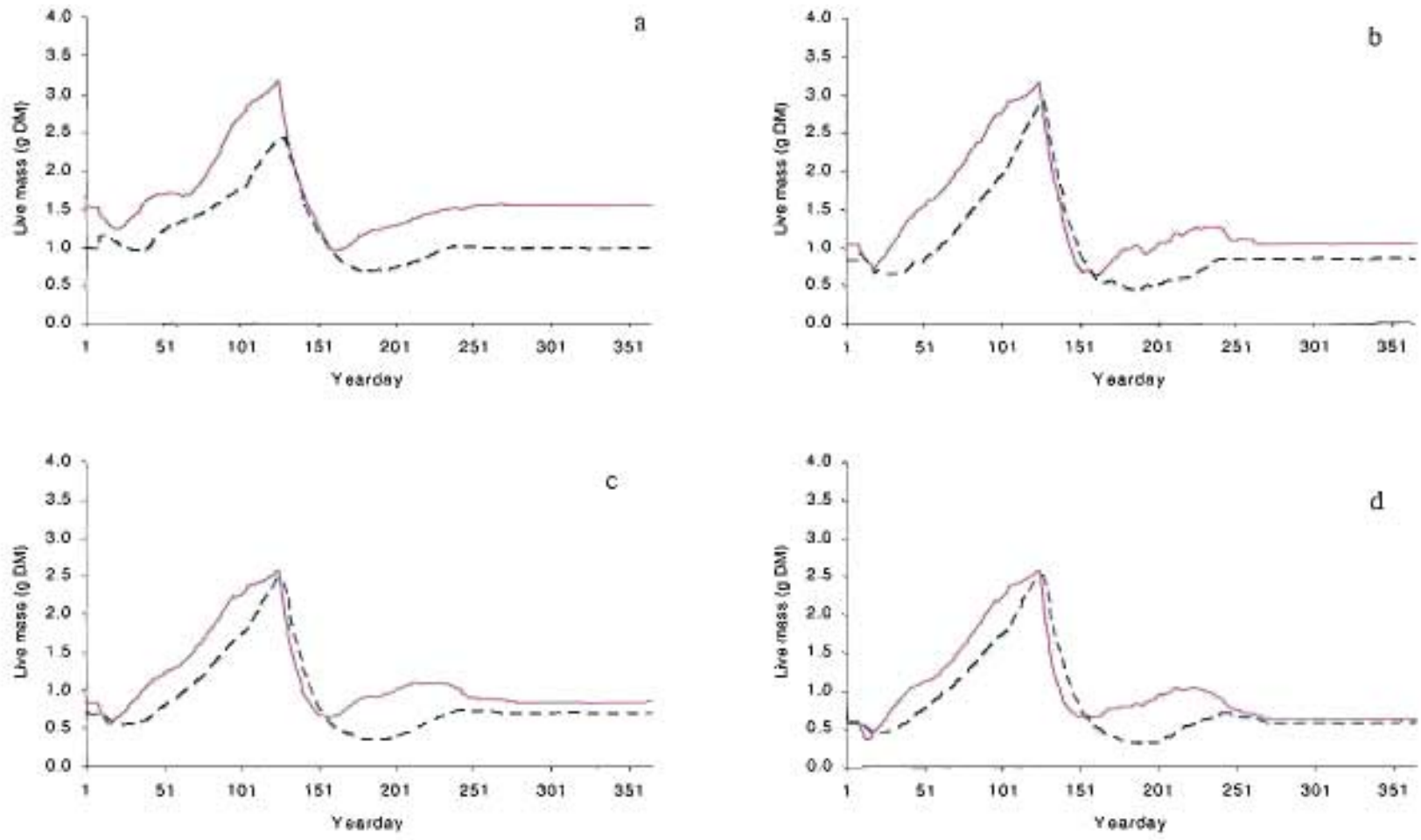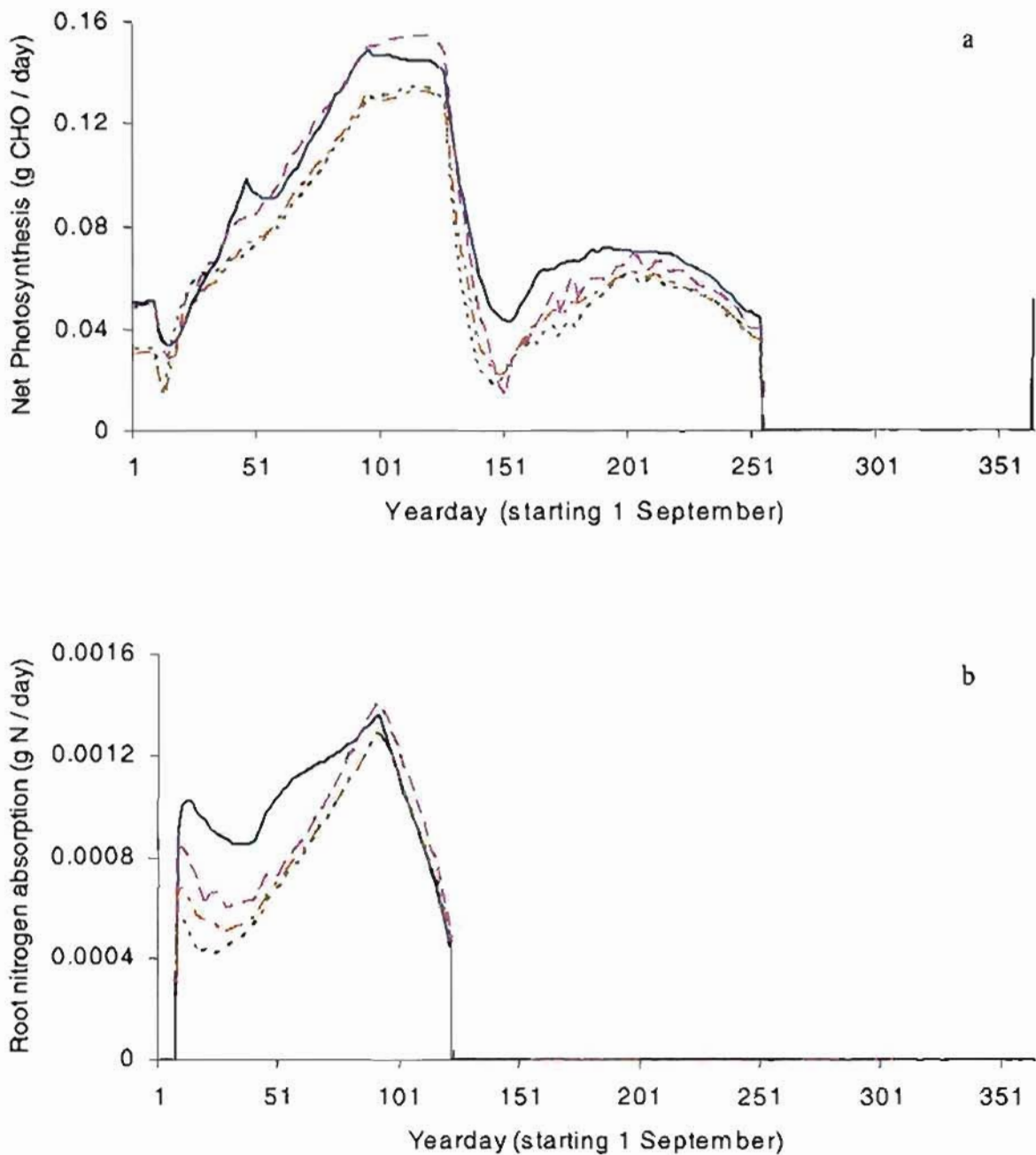
increased with increasing leaf extension rate. This combined evidence indicates that the faster extension rate improves the clone's ability to overcome photosynthetic limitation.

2.1.2 Early growth behaviour

Daily live tiller number and LAI on each clone during the first five years of the simulation is presented in Figure 9.4.

Tiller recruitment on each clone during the first year of growth increased with decreasing leaf extension rate and tiller size. This difference in live object number persisted in the second year and beyond, indicating that the combined growth demand of the individual tillers on the faster leaf extension clones inhibits tiller recruitment by reducing internal resource concentrations below levels necessary for tiller recruitment.

Actual plant growth and nitrogen absorption from the soil during the first season increased with increased leaf extension rate (Figures 9.5). This was because the faster-growing, larger tiller clones were able to grow more quickly during the first season, which increased their ability to accumulate nitrogen and hence growth.

From the second season, the larger number of tillers surviving on the smaller tiller clones ensured that these clones were able to grow more quickly than the clones with larger tillers and faster leaf extension rates. Consequently they are able to accumulate more nitrogen and grow more substantially than clones with larger tillers. This pattern of nitrogen accumulation and growth persisted into subsequent years. This indicates that clones with slower leaf extension rates and smaller tillers are better able to capture nitrogen during the early phase of colonisation than clones with faster leaf extension rates and larger tillers.

In the third season of growth, the clone with slowest leaf extension and smallest tillers actually reduced its growth substantially. This was probably because the large number of surviving tillers at the start of the third season was unsustainable relative to resources. Consequently a large number of tillers died in order to get the clone system closer to available resources. This behaviour of over-shooting and undershooting the resource base was consistently demonstrated over subsequent growth seasons by the clone as a response to the limited resource base. The reason for this behaviour is the delay in terminating photosynthetically less efficient tillers, which leads to inefficient resource allocation during resource-poor periods, and therefore leads to greater tiller mortality. In essence the slowest leaf extension clone behaves more similarly to the proportionate clone described in the
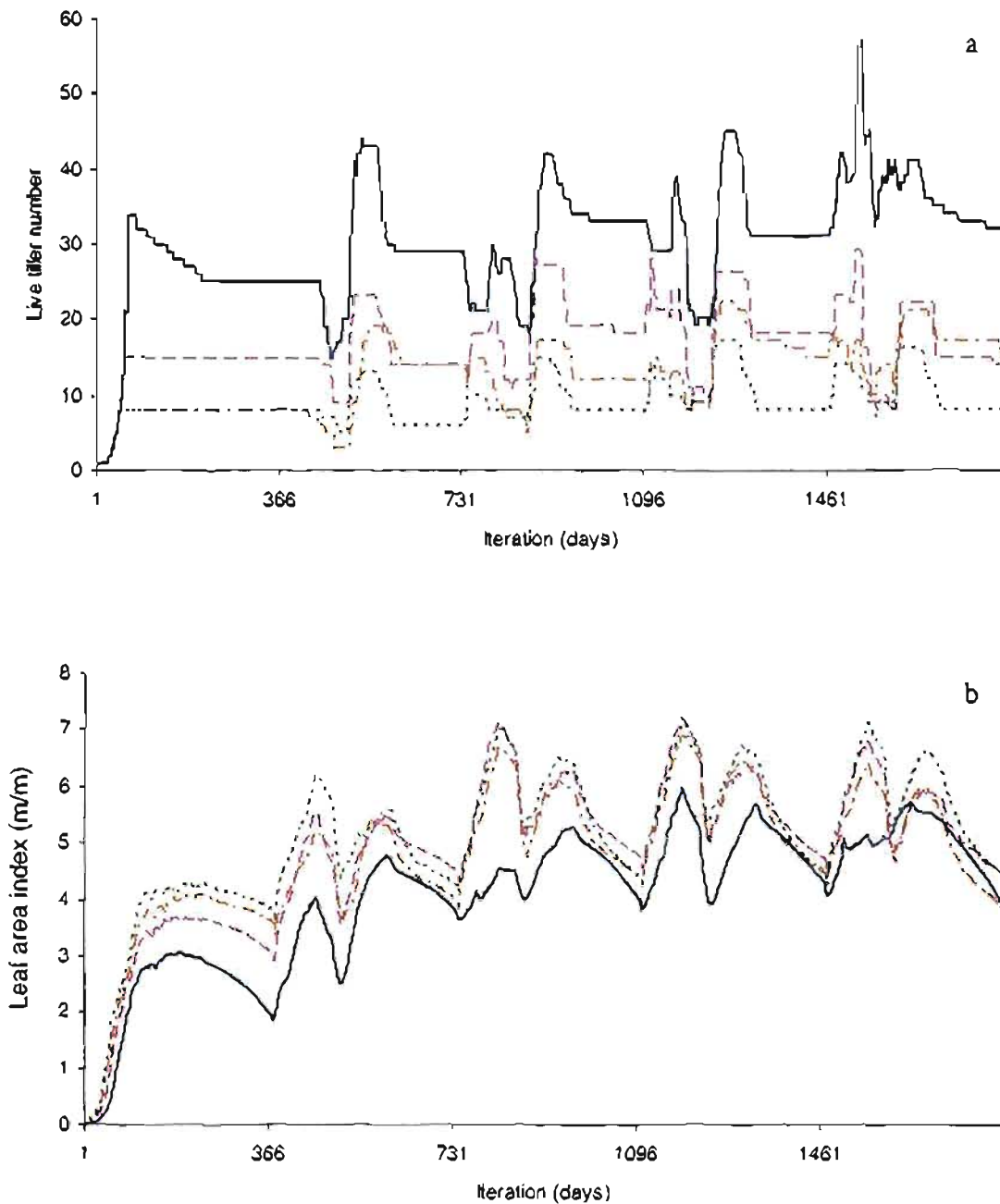
Figure 9.4 Daily live tiller number (a) and daily leaf area index (LAI) (b) during the first five years of simulated clonal growth for four clones of the modelled grass *Themeda triandra* with different leaf extension rates and maximum potential leaf lengths, but identical leaf mass to length ratios. (——— Leaf extension rate x0.5, maximum potential length x0.5; ——— Leaf extension rate x1.0, maximum potential length x1.0; — · — Leaf extension rate x1.5, maximum potential length x1.5; ········· Leaf extension rate x2.0, maximum potential length x2.0.) (Assumptions: Two blades remain alive over winter to ensure spring regrowth. Disproportionate allocation: A_γ = 0.75, A_β = 0.75.) (Environmental conditions: Plant activity during the growing and non-growing season as defined in Section 4.3 of Chapter 4. Growing season proceeds from Yearday 1 to Yearday 242 of each year. Daily soil nitrogen availability as described in Section 3 of Chapter 4.)

Figure 9.5 Annual summed growth (a) and annual nitrogen absorption (b) during the first five years of simulated clonal growth for four clones of the modelled grass *Themeda triandra* with different leaf extension rates and maximum potential leaf lengths, but identical leaf mass to length ratios. (———— Leaf extension rate x0.5, maximum potential length x0.5; – – – Leaf extension rate x1.0, maximum potential length x1.0; — ·— Leaf extension rate x1.5, maximum potential length x1.5; ········ Leaf extension rate x2.0, maximum potential length x2.0.) (Assumptions: Two blades remain alive over winter to ensure spring regrowth. Disproportionate allocation: $A_\gamma = 0.75$, $A_\beta = 0.75$.) (Environmental conditions: Plant activity during the growing and non-growing season as defined in Section 4.3 of Chapter 4. Growing season proceeds from Yearday 1 to Yearday 242 of each year. Daily soil nitrogen availability as described in Section 3 of Chapter 4.)

previous chapter than the other faster leaf extension clones. In addition the clone is slower to overcome light limitation when new tillers are forced to emerge through older dead material, which exacerbates the resource limitation and increases tiller mortality.

The three taller clones took three years to occupy the available resource space, as indicated by the daily LAI above the ground (Figure 9.5), while the shortest clone took an extra year to occupy the available resource space. The latter also achieved lower LAI values than the other three clones with larger tillers, because it allocated more resources to stem material.

2.2 Tillers with the same height but different leaf thickness

2.2.1 Average annual behaviour

Table 9.2 shows summarised data for the four clones grown with identical leaf extension rates and maximum potential leaf lengths, but different mass-to-length ratios. This created four tillers of identical height pot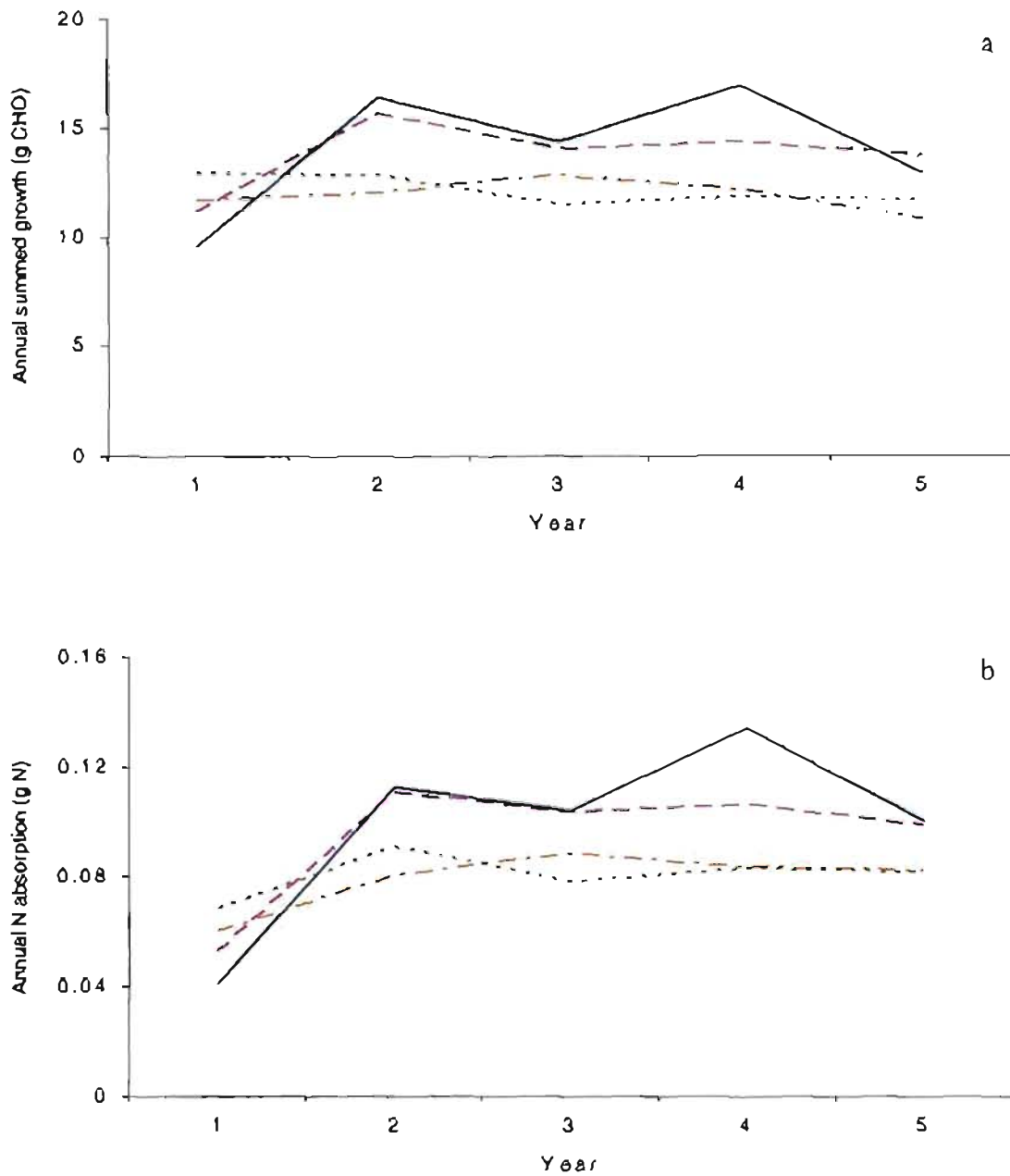ential but with thin through to thick leaved tillers which caused them to have different daily growth rates. The data indicates that the four clones had similar average annual nitrogen absorption, net photosynthesis and summed growth estimates, although the clone with thinnest leaves was notably less productive than the other three clones.

Maximum annual organ mass values varied across the clones. Leaf mass (blade mass and sheath mass) was lowest on the clone with thinnest leaves, and highest on the clone with thickest leaves. By contrast internode mass and flower mass was larger on the clones with thinner leaves, which reflected the fact that the clones with thinner leaves sustained more tillers and more inflorescences each year than the clones with thicker leaves.

Live object number

The average live number of objects on each clone across a year was highest on the clone with thinnest leaves and decreased across the four clones as leaf thickness increased (Figure 9.6). This is reflects the fact that the nitrogen resource in the system is restricted and therefore more smaller tillers could be maintained and grow on the available resources than larger tillers. The greater flower production on the clones with thinner leaves probably

153
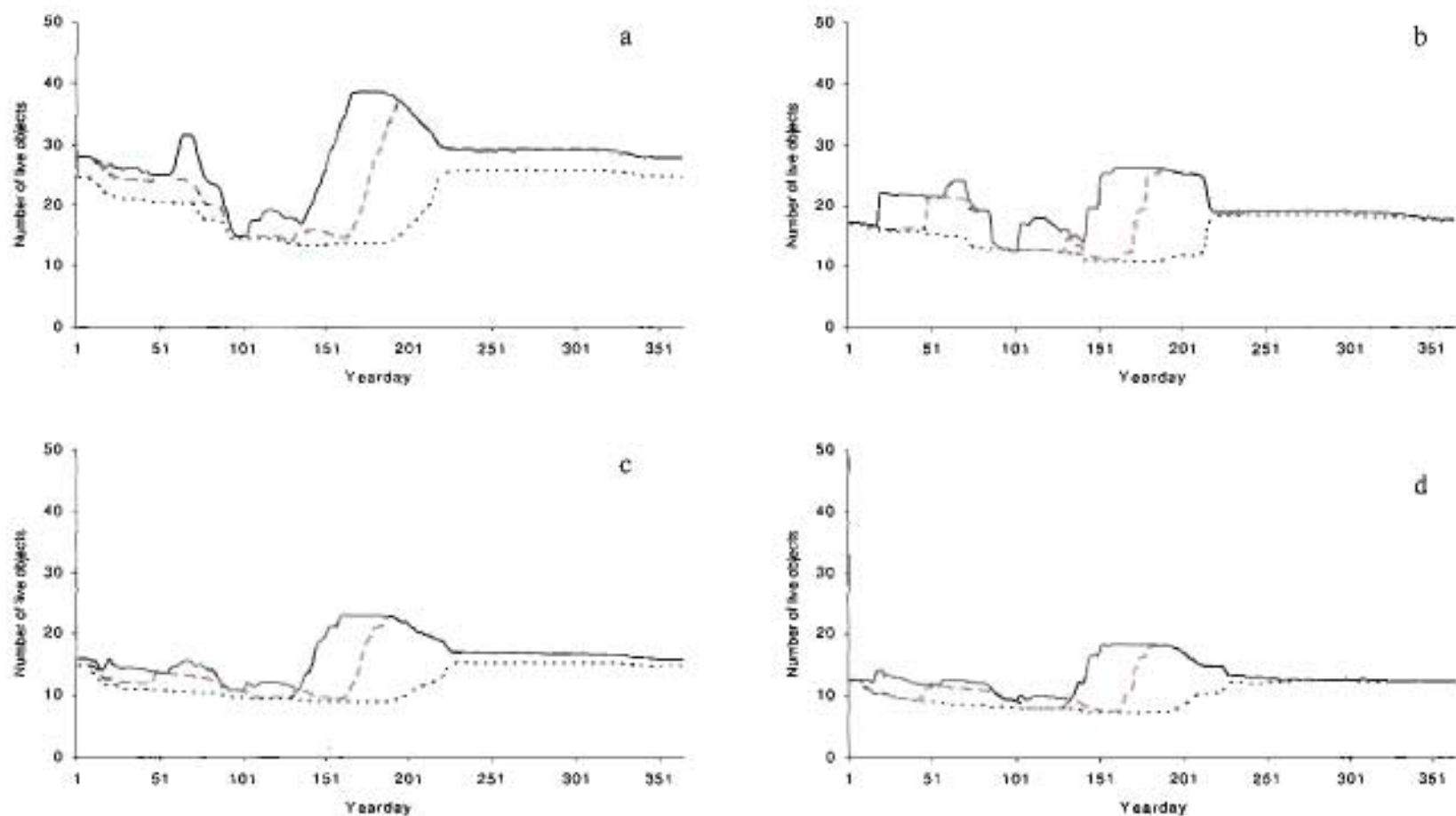
Figure 9.6 Average clonal daily number of live tillers (———), live ramets (— — —) and live ramet groups (········) on four clones of the modelled grass *Themeda triandra* with identical leaf extension rates and maximum potential leaf lengths, but different leaf mass to length ratios. a. Leaf mass to length ratio x0.5; b Leaf mass to length ratio x1.0; c. Leaf mass to length ratio x1.5; d. Leaf mass to length ratio x2.0. (Assumptions: Two blades remain alive over winter to ensure spring regrowth. Disproportionate allocation: $A_r = 0.75$, $A_\delta = 0.75$.) (Environmental conditions: Plant activity during the growing and non-growing season as defined in Section 4.3 of Chapter 4. Growing season proceeds from Yearday 1 to Yearday 242 of each year. Daily soil nitrogen availability as described in Section 3 of Chapter 4.)

results directly from the fact that they are able to sustain more live tillers through winter prior to floral induction and therefore had a greater number of potential flowering tillers.

The distribution of tiller recruitment events was similar to those recorded for the previous clones. In fact the live object curves for each clone was remarkably similar to its tiller size equivalent in the previous set of simulations (Figure 9.1). This indicates that tiller survival in an environment with restricted resources is inversely related to tiller potential size.

Live clonal mass and daily resource capture

The clone with thinnest leaves started spring with greater live biomass then the other three clones, which had similar values (Figure 9.7). However the leaf mass growth rates of the thicker-leafed clones were progressively faster during the spring period and these overcame light limitation more quickly than the thinner leafed clones. This is indicated by their greater root-to-shoot ratios over the spring period. Therefore the thicker leafed clones actually achieved higher biomasses during flowering.

The regrowth rate differences ensured that the three thicker-leafed clones accumulated more nitrogen than the thinnest-leafed clone across the growing season even though they started with lower live mass values at the beginning of the growing season (Figure 9.8b). Net photosynthetic production was lowest on the clone with thinnest leaves, while the remaining three clones showed similar photosynthetic abilities (Figure 9.8a).

The live clonal biomass trough after flowering was most severe on the clone with thickest leaves and least severe on the clone with thinnest leaves. This probably reflects the effect of tiller size and live tiller number, where death of mature tillers on the clone with thinnest leaves would have caused a proportionately smaller drop in clonal biomass per unit than would occur on the clone with thickest leaves.

154

Table 9.2   Average performance of modelled clones of *Themeda triandra* with the same leaf extension rates and leaf maximum potential lengths, but different mass-to-length ratios. Tillers all have identical potential height, but their potential masses range from light to heavy.

	Allocation procedure							
	Light						**Heavy**	
Leaf extension rate	x1.0		x1.0		x1.0		x1.0	
Potential leaf length	x1.0		x1.0		x1.0		x1.0	
Mass-to-length ratio	x0.5		x1.0		x1.5		x2.0	
	Mean	S.E.	Mean	S.E.	Mean	S.E.	Mean	S.E.
Average reproductive tiller data								
Number of flowering tillers	9.00	0.25	7.09	0.020	5.95	0.35	5.41	0.25
Maximum blade mass (g tiller^{-1})	0.063	0.001	0.126	0.003	0.155	0.003	0.194	0.004
Maximum sheath mass (g tiller^{-1})	0.022	0.000	0.043	0.001	0.053	0.002	0.067	0.002
Max internode mass (g tiller^{-1})	0.190	0.004	0.214	0.005	0.219	0.006	0.227	0.007
Maximum flower mass (g tiller^{-1})	0.030	0.001	0.041	0.001	0.045	0.001	0.048	0.001
Maximum culm length (mm)	514.04	8.38	564.07	12.41	557.40	14.45	565.52	15.06
Average clonal organ mass								
Maximum blade mass (g)	0.677	0.018	1.082	0.021	1.016	0.041	1.158	0.031
Maximum sheath mass (g)	0.223	0.006	0.336	0.005	0.333	0.011	0.380	0.006
Maximum internode mass (g)	1.728	0.046	1.512	0.018	1.279	0.050	1.203	0.029
Maximum flower mass (g)	0.273	0.007	0.285	0.004	0.263	0.011	0.254	0.006
Average clonal annual production								
Net photosynthesis (g CHO)	17.109	0.318	19.337	0.159	18.646	0.414	19.155	0.238
N absorption (g N)	0.094	0.001	0.101	0.001	0.099	0.002	0.101	0.001
Summed growth (g CHO)	12.280	0.236	13.683	0.094	13.438	0.320	13.847	0.197
Summed growth deficit (g CHO)	113.556	2.527	122.242	2.014	104.197	2.964	106.316	3.218
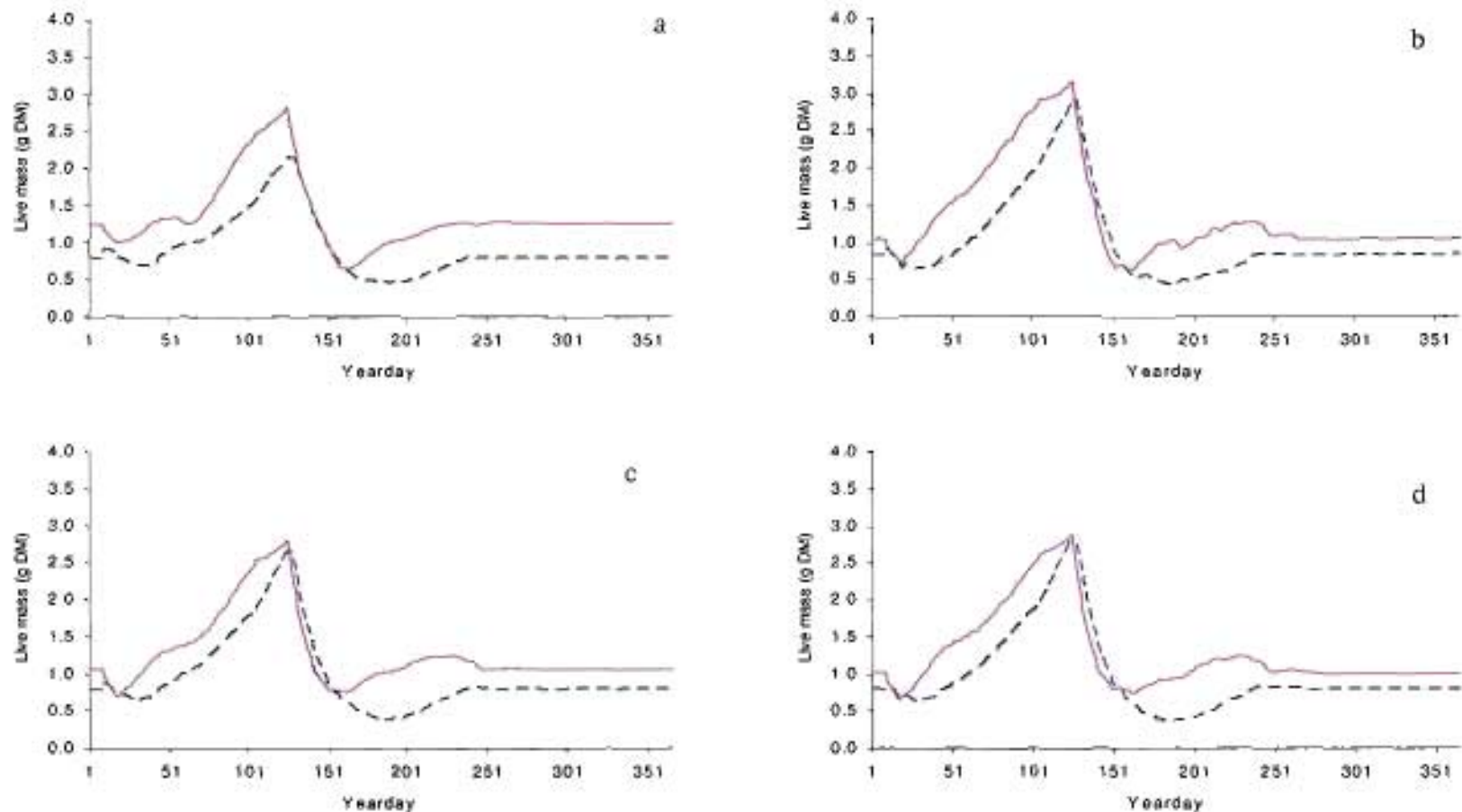
Figure 9.7   Average daily live shoot mass (————) and live root mass (— — —) on four clones of the modelled grass *Themeda triandra* with identical leaf extension rates and maximum potential leaf lengths, but different leaf mass to length ratios. a. Leaf mass to length ratio x0.5; b Leaf mass to length ratio x1.0; c. Leaf mass to length ratio x1.5; d. Leaf mass to length ratio x2.0. (Assumptions: Two blades remain alive over winter to ensure spring regrowth. Disproportionate allocation: $A_r = 0.75$, $A_s = 0.75$.) (Environmental conditions: Plant activity during the growing and non-growing season as defined in Section 4.3 of Chapter 4. Growing season proceeds from Yearday 1 to Yearday 242 of each year. Daily soil nitrogen availability as described in Section 3 of Chapter 4.)

Figure 9.8   Average daily net photosynthetic production (a) and soil N absorption (b) on four clones of the modelled grass *Themeda triandra* with identical leaf extension rates and maximum potential leaf lengths, but different leaf mass to length ratios. (———— Leaf mass to length ratio x0.5; — — — Leaf mass to length ratio x1.0; — · — Leaf mass to length ratio x1.5; ········ Leaf mass to length ratio x2.0.) (Assumptions: Two blades remain alive over winter to ensure spring regrowth. Disproportionate allocation: $A_\gamma = 0.75$, $A_\beta = 0.75$.) (Environmental conditions: Plant activity during the growing and non-growing season as defined in Section 4.3 of Chapter 4. Growing season proceeds from Yearday 1 to Yearday 242 of each year. Daily soil nitrogen availability as described in Section 3 of Chapter 4.)

2.2.2 Early growth behaviour

Daily live tiller number and LAI on each clone during the first five years of the simulation are presented in Figure 9.9. Live tillers recruited on each clone during the first season followed identical patterns to the clones with tiller size equivalents in the first set of simulations (Figure 9.4). Clones with smaller tillers recruited more secondary tillers than clones with large tillers. This confirms that daily resource demand placed by existing growing tillers restricts the rate at which secondary tillers may be recruited, by limiting the number of days when internal resource concentrations exceed the minimum amounts required for secondary recruitment.

Live tiller number on the clone with thinnest leaves was always higher than for the other three clones. By contrast the live tiller number on the remaining three clones was interchangeable across the first five years, although the clone with thickest leaves usually had the lowest number of live tillers on any day in the time period.

Leaf area index was highest on the clone with thickest leaves and decreased with decreasing leaf thickness (Figure 9.9). This indicates that the clone with thickest leaves also accumulated the most leaf biomass. The LAI of the clone with thinnest leaves was notably less than the other three clones. This suggests that it had much greater photosynthetic efficiency per unit of leaf biomass, which allowed it to achieve comparable (though certainly less) photosynthetic production to the other three clones.

Nitrogen absorption and growth in the first season was greatest on the clone with thickest leafs and fastest tiller daily growth rate and decreased with decreasing leaf thickness and tiller daily growth rate (Figure 9.10). This was identical to the values found in the first set of four clones, which had the identical distribution of daily tiller growth rates. However from the second year on, annual growth productivity and nitrogen absorption order was interchangeable, indicating that no clone obtained an advantage in resource capture during the early growth period.

All four clones took three years to occupy the available resource space, as indicated by the daily LAI above the ground (Figure 9.9), which indicates that none of the four clones reached resource occupation more quickly than the others.

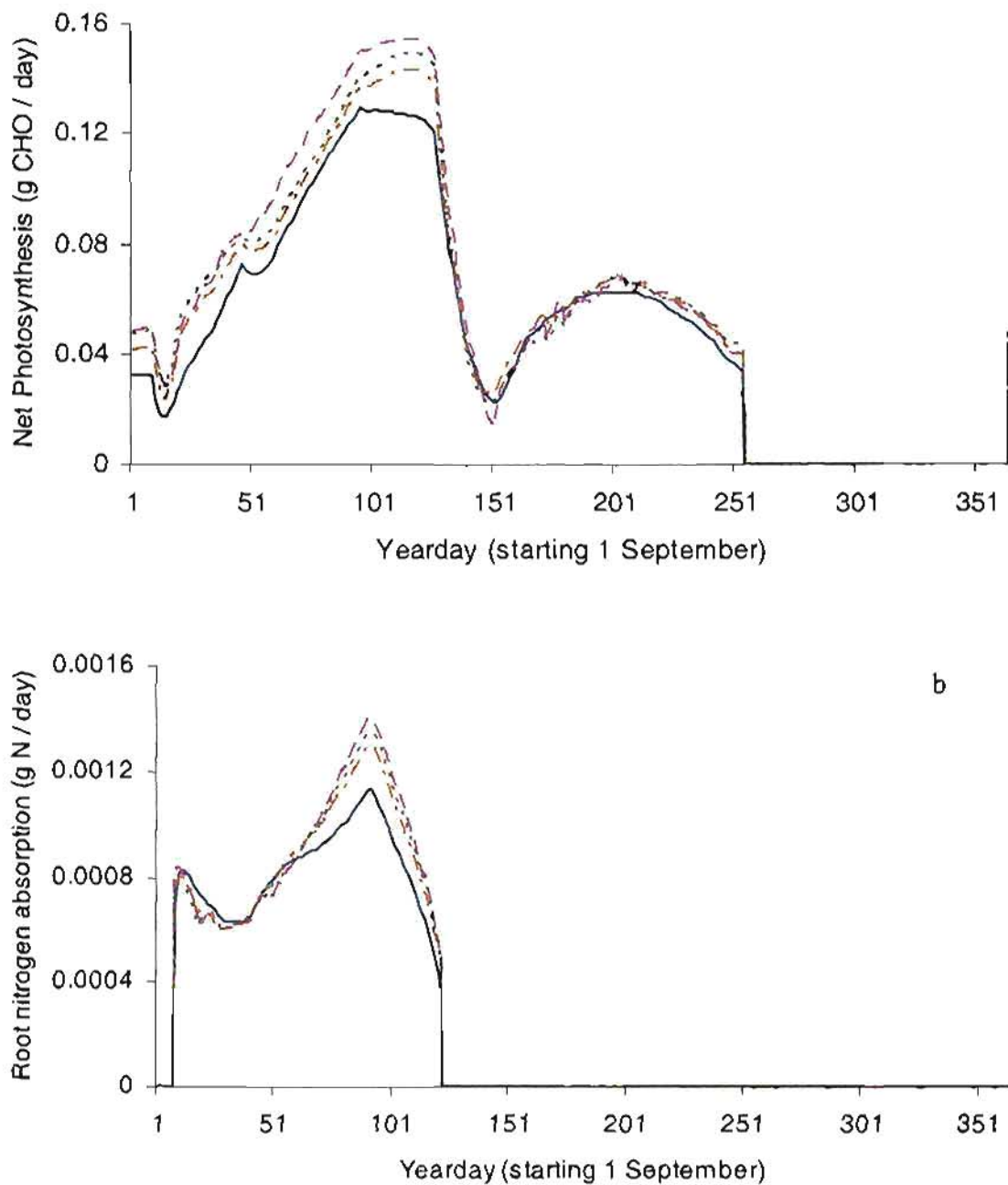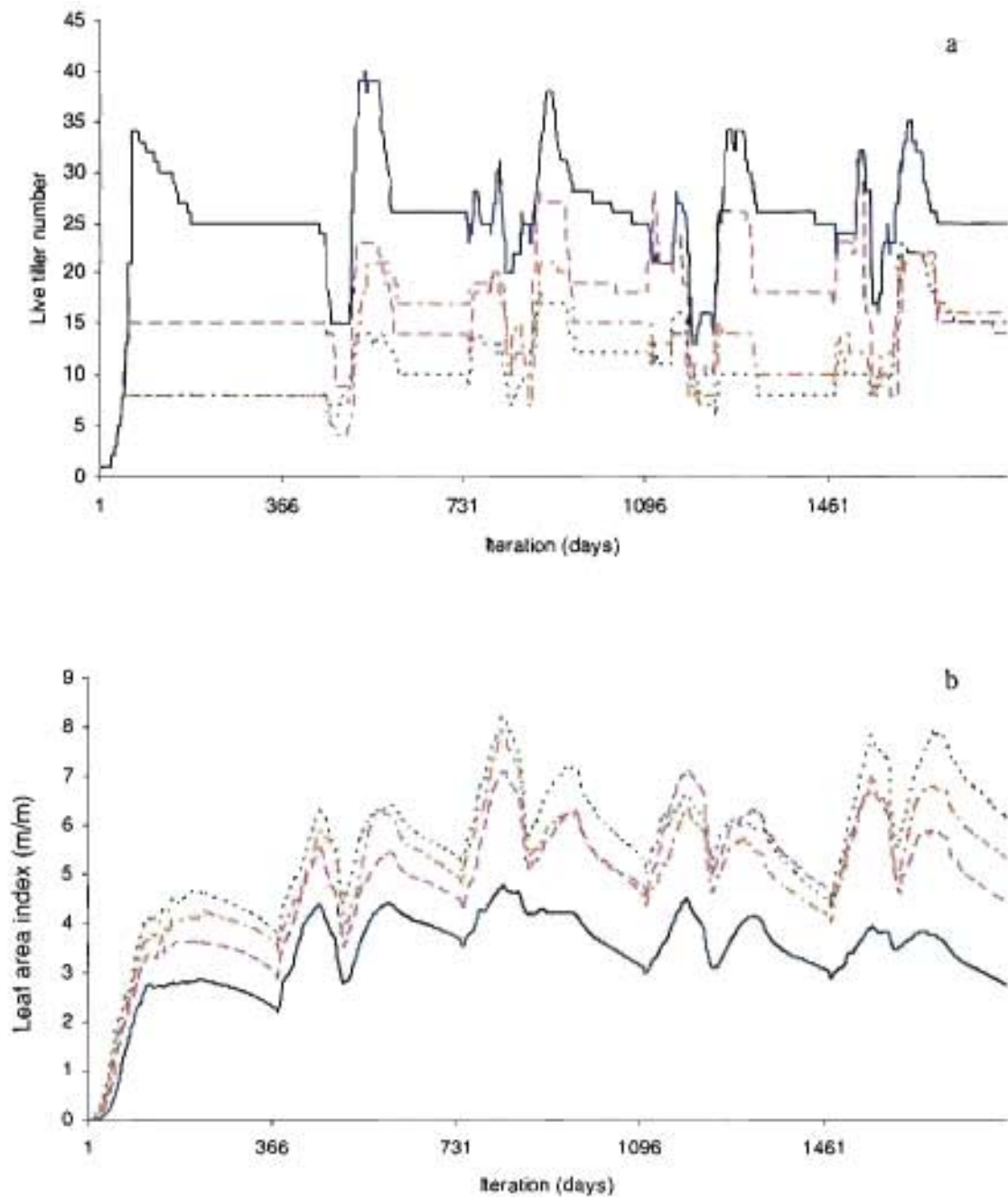**Figure 9.9** Daily live tiller number (a) and daily leaf area index (LAI) (b) during the first five years of simulated clonal growth for four clones of the modelled grass *Themeda triandra* with identical leaf extension rates and maximum potential leaf lengths, but different leaf mass to length ratios. (———— Leaf mass to length ratio x0.5; — — — Leaf mass to length ratio x1.0; — · — Leaf mass to length ratio x1.5; ········ Leaf mass to length ratio x2.0.) (Assumptions: Two blades remain alive over winter to ensure spring regrowth. Disproportionate allocation: $A_\gamma = 0.75$, $A_\delta = 0.75$.) (Environmental conditions: Plant activity during the growing and non-growing season as defined in Section 4.3 of Chapter 4. Growing season proceeds from Yearday 1 to Yearday 242 of each year. Daily soil nitrogen availability as described in Section 3 of Chapter 4.)

Figure 9.10   Annual summed growth (a) and annual nitrogen absorption (b) during the first five years of simulated clonal growth for four clones of the modelled grass *Themeda triandra* with identical leaf extension rates and maximum potential leaf lengths, but different leaf mass to length ratios. (————— Leaf mass to length ratio x0.5; — — — Leaf mass to length ratio x1.0; — · — Leaf mass to length ratio x1.5; ········ Leaf mass to length ratio x2.0.) (Assumptions: Two blades remain alive over winter to ensure spring regrowth. Disproportionate allocation: $A_\gamma = 0.75$, $A_\beta = 0.75$.) (Environmental conditions: Plant activity during the growing and non-growing season as defined in Section 4.3 of Chapter 4. Growing season proceeds from Yearday 1 to Yearday 242 of each year. Daily soil nitrogen availability as described in Section 3 of Chapter 4.)

2.3   Tillers that range from short-and-fat to tall-and-thin

2.3.1   Average annual behaviour

Table 9.3 shows summarised data for the four clones which had identical potential tiller masses and daily mass growth rates, but grown with different leaf extension rates and maximum potential leaf lengths, and inverted mass-to-length ratios.

The clone with short, fat tillers accumulated substantially more nitrogen, had greater net photosynthetic production and greater annual growth productivity than the other clones with taller and thinner tillers. These productivity variables decreased substantially and progressively with increased tiller height and thinness.

The number of flowering tillers was highest on the clone with short, fat tillers and decreased across the clones with increased tiller height and thinness. Maximum clonal biomass (blades, sheaths, internodes, flowers) at any time during the year was greatest on the clone with second shortest tillers, although values were quite similar to those achieved by the clone with shortest tillers. The two clones with shorter, fatter tillers achieved substantially greater live biomass values than the two clones with taller, thinner tillers.

Live object number

Average annual daily live object number was highest on the clone with short, fat tillers and decreased across the clones with increasing tiller height and thinness (Figure 9.11). Notably the difference in live object number between the clone with short, fat tillers and the clone with tall, thin tillers was much smaller than had occurred across the clones in the two previous sets of simulations (Figure 9.1 and 9.6). This confirms that the number of tillers that live within the environmental resource limits is inversely proportional to the potential mass size of individual tillers. The differences in live tillers maintained by the clone with short, fat tillers from the clone with tall, thin tillers occurred because the former accumulated more environmental nitrogen and so increased its resource base relative to that of the clone with tall, thin tillers.

157

Table 9.3 Average performance of modelled clones of *Themeda triandra* with different leaf extension rates and leaf maximum potential lengths, and inverse mass-to-length ratios respectively. Tillers range from potentially short to potentially tall, but with the same potential mass

	Allocation procedure							
	Short						**Tall**	
Leaf extension rate	**x0.5**		**x1.0**		**x1.5**		**x2.0**	
Potential leaf length	x0.5		x1.0		x1.5		x2.0	
Mass-to-length ratio	x2.0		x1.0		x0.67		x0.5	
	Mean	S.E.	Mean	S.E.	Mean	S.E.	Mean	S.E.
Average reproductive tiller data								
Number of flowering tillers	8.73	0.47	7.09	0.020	6.36	0.39	6.14	0.32
Maximum blade mass (g tiller^{-1})	0.103	0.001	0.126	0.003	0.105	0.004	0.106	0.004
Maximum sheath mass (g tiller^{-1})	0.033	0.001	0.043	0.001	0.035	0.002	0.035	0.002
Max internode mass (g tiller^{-1})	0.178	0.004	0.214	0.005	0.192	0.008	0.191	0.008
Maximum flower mass (g tiller^{-1})	0.034	0.001	0.041	0.001	0.038	0.002	0.037	0.002
Maximum culm length (mm)	468.98	8.85	564.07	12.41	505.56	18.43	508.27	18.16
Average clonal organ mass								
Maximum blade mass (g)	1.094	0.036	1.082	0.021	0.735	0.033	0.723	0.032
Maximum sheath mass (g)	0.338	0.009	0.336	0.005	0.235	0.009	0.235	0.010
Maximum internode mass (g)	1.550	0.066	1.512	0.018	1.182	0.049	1.162	0.050
Maximum flower mass (g)	0.295	0.012	0.285	0.004	0.229	0.009	0.223	0.010
Average clonal annual production								
Net photosynthesis (g CHO)	22.161	0.386	19.337	0.159	15.286	0.491	14.612	0.493
N absorption (g N)	0.121	0.002	0.101	0.001	0.082	0.002	0.078	0.003
Summed growth (g CHO)	15.950	0.258	13.683	0.094	11.041	0.365	10.544	0.360
Summed growth deficit (g CHO)	128.601	3.647	122.242	2.014	94.871	4.267	90.397	3.553
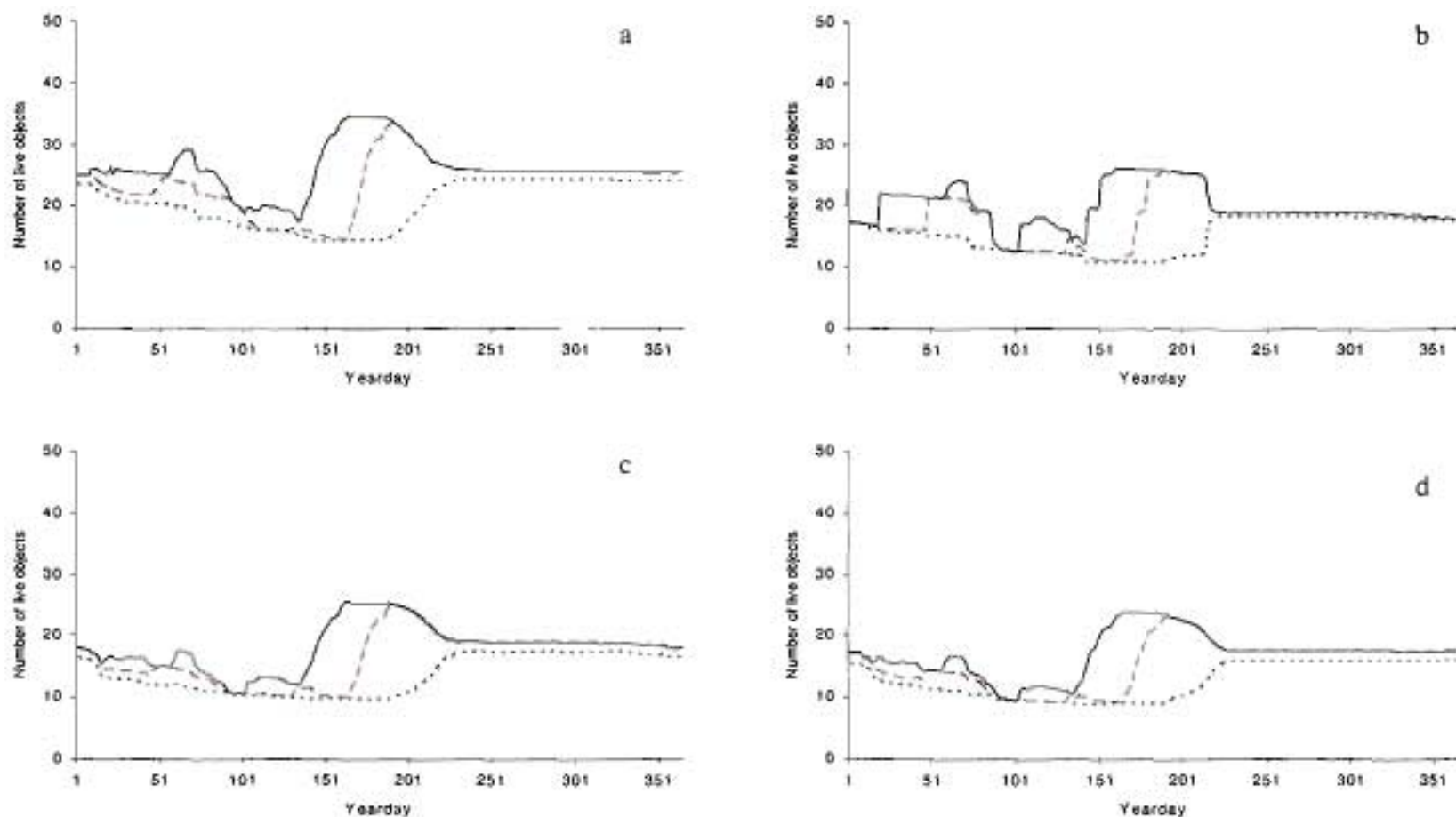
Figure 9.11 Average clonal daily number of live tillers (————), live ramets (— — —) and live ramet groups (··········) on four clones of the modelled grass *Themeda triandra* with different leaf extension rates and maximum potential leaf lengths, and inverted leaf mass to length ratios. a. Leaf extension rate x0.5, Leaf mass to length ratio x2.0; b Leaf extension rate x1.0, Leaf mass to length ratio x1.0; c. Extension rate x1.5, Leaf mass to length ratio x0.67; d. Extension rate x2.0, Leaf mass to length ratio x0.5. (Assumptions: Two blades remain alive over winter to ensure spring regrowth. Disproportionate allocation: $A_r = 0.75$, $A_\theta = 0.75$.) (Environmental conditions: Plant activity during the growing and non-growing season as defined in Section 4.3 of Chapter 4. Growing season proceeds from Yearday 1 to Yearday 242 of each year. Daily soil nitrogen availability as described in Section 3 of Chapter 4.)

Average daily live biomass was highest on the clone with short, fat tillers and decreased across the clones with increased tiller height and thinness (Figure 9.12). This effect was most notable at the end of winter, when shoot biomass on that clone was about 1.5 times greater than on the other three clones. This difference allowed the clone with short, fat tillers to produce greater amounts of photosynthate in early spring than the other three clones (Figure 9.13). In addition the said clone accumulated greater amounts of nitrogen than the other three clones because it had greater root biomass in spring as well.

The clone with short, fat tillers, had the lowest root-to-shoot ratio. The remaining three clones had similar, higher root-to-shoot ratios, but these also decreased to lower biomass values during the trough after flowering. The combined evidence indicates that there is a direct trade-off in clonal bunchgrasses between the ability to capture nitrogen and the ability to grow tall and overcome photosynthetic limitation by competitors.

2.3.2   Early growth behaviour

Daily live tiller number and LAI on each clone during the first five years of the simulation are presented in Figure 9.14. All four clones recruit the same number of tillers during the first season of growth because their tillers have identical daily growth resource demands. From the second year the clone with short, fat tillers starts to increase its number of live tillers above numbers achieved by the other clones, but there is still a larger amount of variation in the order of clonal live tiller number in each season, indicating the effect of discrete growth processes.

The order of highest LAI values also changes over the first five seasons, although the clone with short, fat tillers becomes increasingly the clone with greatest LAI, indicating its greater productivity. The taller three clones occupied the available resource space within three years, while the clone with short, fat tillers took an extra year to occupy the resource space.

Annual nitrogen capture and annual summed growth were very similar for the four clones in the first season of growth because they accumulated biomass at the same rate during that season because of identical tiller daily growth rates (Figure 9.15). However from the second season, the two clones with shorter, fatter tillers absorbed more nitrogen and had

159
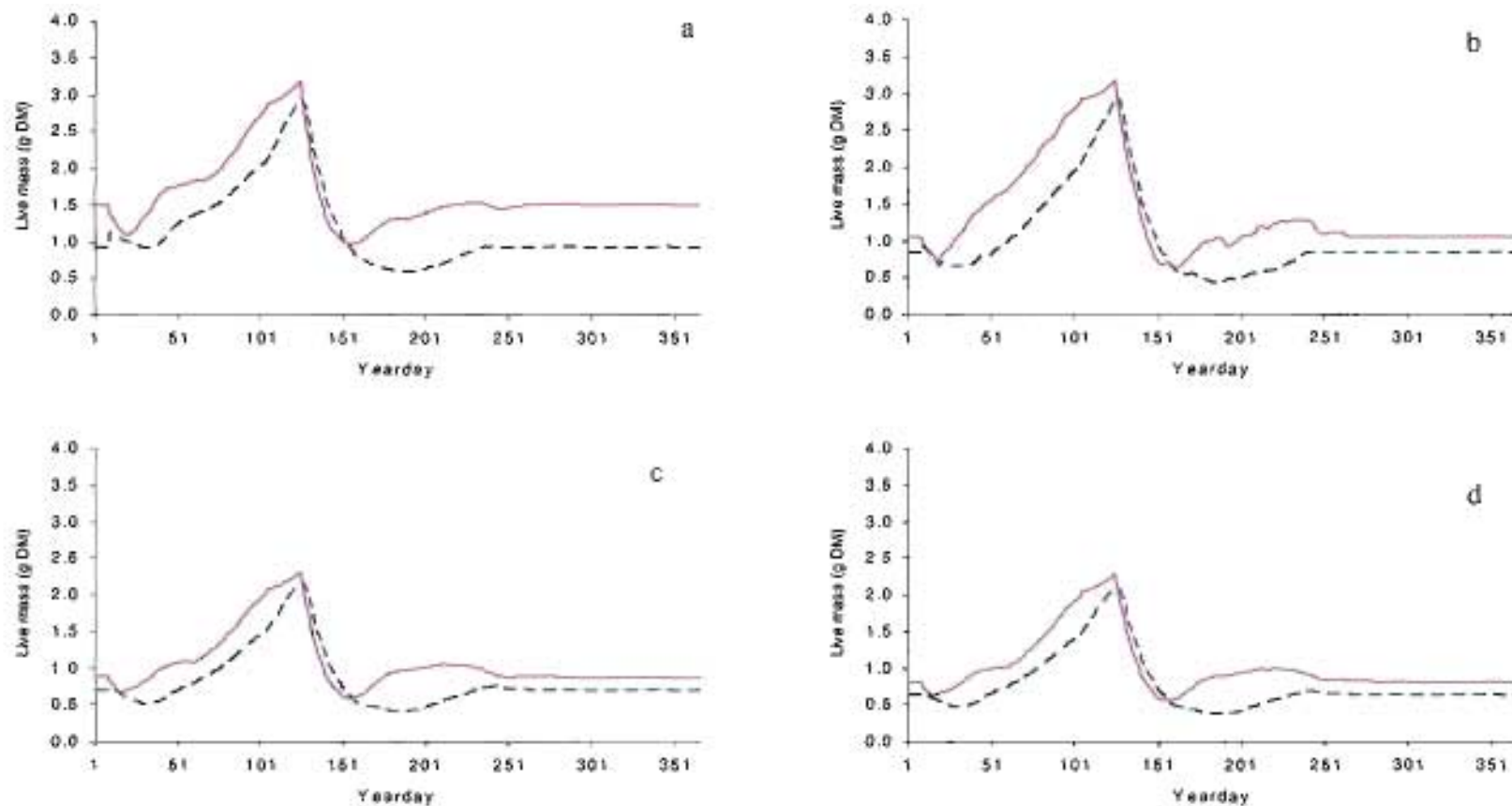
Figure 9.12   Average daily live shoot mass (————) and live root mass (– – –) on four clones of the modelled grass *Themeda triandra* with different leaf extension rates and maximum potential leaf lengths, and inverted leaf mass to length ratios. a. Leaf extension rate x0.5, Leaf mass to length ratio x2.0; b Leaf extension rate x1.0, Leaf mass to length ratio x1.0; c. Extension rate x1.5, Leaf mass to length ratio x0.67; d. Extension rate x2.0, Leaf mass to length ratio x0.5. (Assumptions: Two blades remain alive over winter to ensure spring regrowth. Disproportionate allocation: $A_v = 0.75$, $A_\delta = 0.75$.) (Environmental conditions: Plant activity during the growing and non-growing season as defined in Section 4.3 of Chapter 4. Growing season proceeds from Yearday 1 to Yearday 242 of each year. Daily soil nitrogen availability as described in Section 3 of Chapter 4.)

Figure 9.13 Average daily net photosynthetic production (a) and soil N absorption (b) on four clones of the modelled grass *Themeda triandra* with different leaf extension rates and maximum potential leaf lengths, and inverted leaf mass to length ratios. (———— Leaf extension rate x0.5, Leaf mass to length ratio x2.0; — — — Leaf extension rate x1.0, Leaf mass to length ratio x1.0; — · — Leaf extension rate x1.5, Leaf mass to length ratio x0.67; ········ Leaf extension rate x2.0, Leaf mass to length ratio x0.5.) (Assumptions: Two blades remain alive over winter to ensure spring regrowth. Disproportionate allocation: $A_\gamma = 0.75$, $A_\beta = 0.75$.) (Environmental conditions: Plant activity during the growing and non-growing season as defined in Section 4.3 of Chapter 4. Growing season proceeds from Yearday 1 to Yearday 242 of each year. Daily soil nitrogen availability as described in Section 3 of Chapter 4.)

Figure 9.14 Daily live tiller number (a) and daily leaf area index (LAI) (b) during the first five years of simulated clonal growth for four clones of the modelled grass *Themeda triandra* with different leaf extension rates and maximum potential leaf lengths, and inverted leaf mass to length ratios. (———— Leaf extension rate x0.5, Leaf mass to length ratio x2.0; — — — Leaf extension rate x1.0, Leaf mass to length ratio x1.0; — · — Leaf extension rate x1.5, Leaf mass to length ratio x0.67; ········ Leaf extension rate x2.0, Leaf mass to length ratio x0.5.) (Assumptions: Two blades remain alive over winter to ensure spring regrowth. Disproportionate allocation: A_γ = 0.75, A_β = 0.75.) (Environmental conditions: Plant activity during the growing and non-growing season as defined in Section 4.3 of Chapter 4. Growing season proceeds from Yearday 1 to Yearday 242 of each year. Daily soil nitrogen availability as described in Section 3 of Chapter 4.)

Figure 9.15 Annual summed growth (a) and annual nitrogen absorption (b) during the first five years of simulated clonal growth for four clones of the modelled grass *Themeda triandra* with different leaf extension rates and maximum potential leaf lengths, and inverted leaf mass to length ratios (——— Leaf extension rate x0.5, Leaf mass to length ratio x2.0; — — — Leaf extension rate x1.0, Leaf mass to length ratio x1.0; — · — Leaf extension rate x1.5, Leaf mass to length ratio x0.67; ········ Leaf extension rate x2.0, Leaf mass to length ratio x0.5.) (Assumptions: Two blades remain alive over winter to ensure spring regrowth. Disproportionate allocation: $A_\gamma = 0.75$, $A_\beta = 0.75$.) (Environmental conditions: Plant activity during the growing and non-growing season as defined in Section 4.3 of Chapter 4. Growing season proceeds from Yearday 1 to Yearday 242 of each year. Daily soil nitrogen availability as described in Section 3 of Chapter 4.)
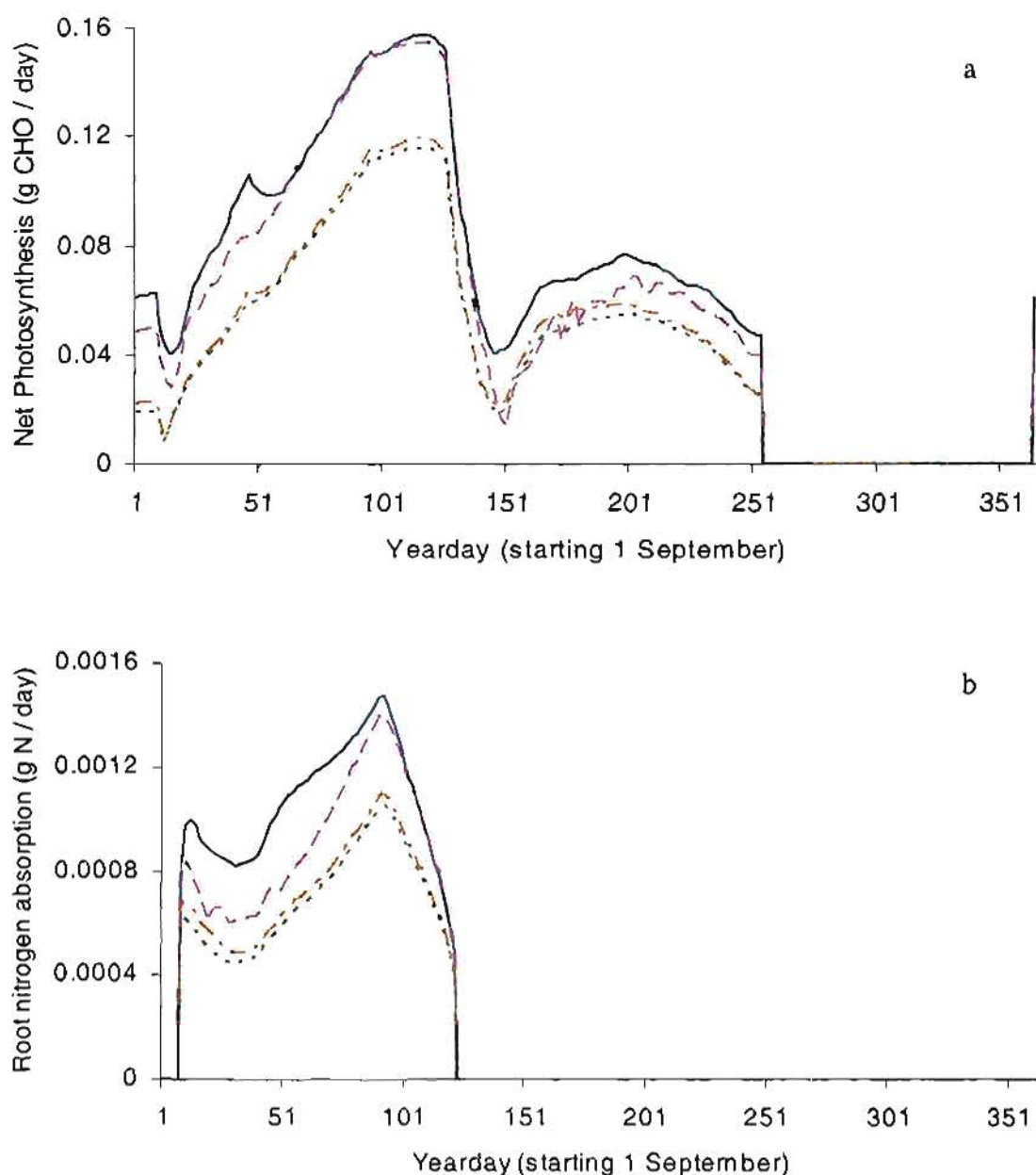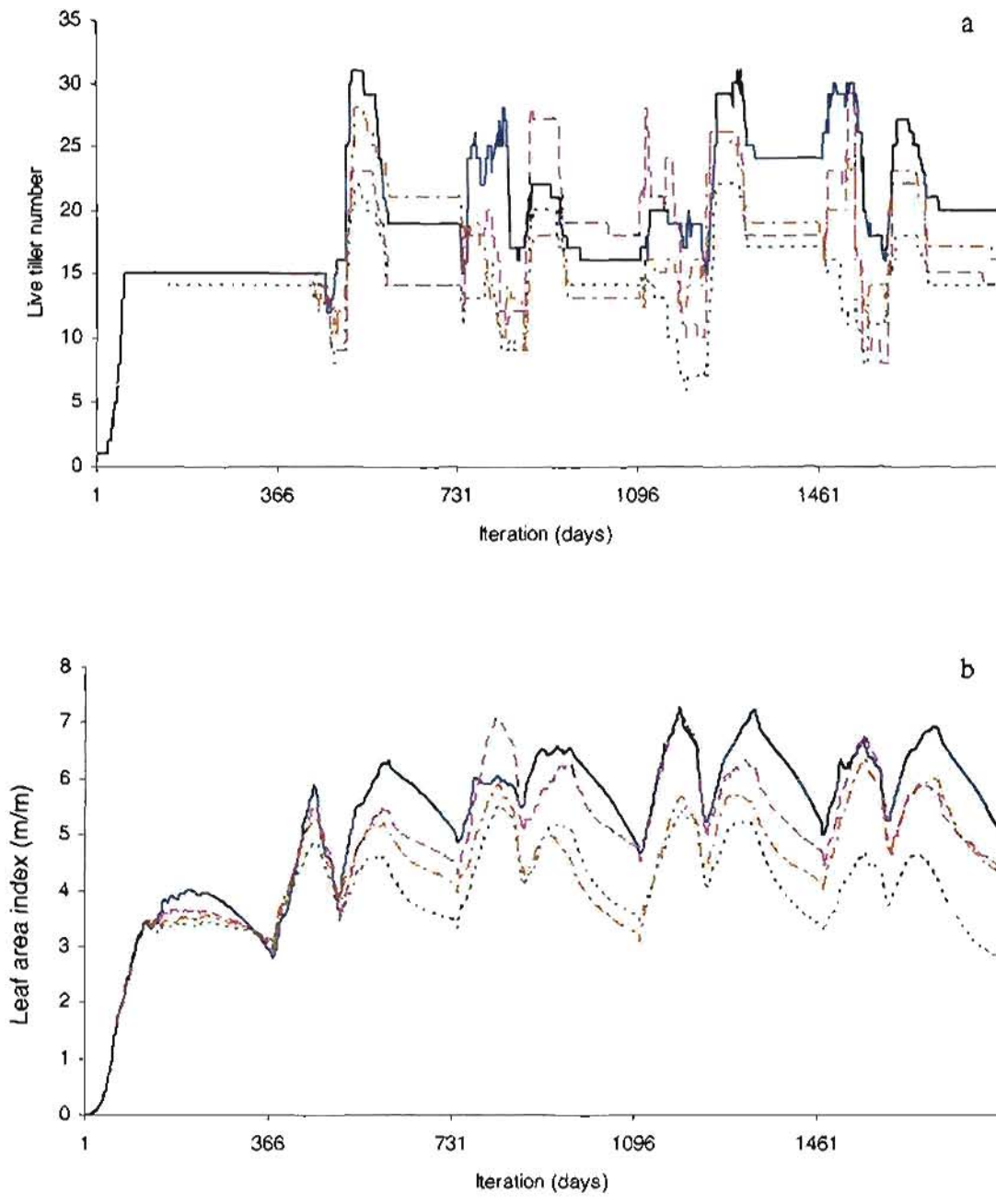
greater annual productivity than the two clones with taller, thinner tillers. This indicates that the clones with shorter, fatter tillers were better able to accumulate and utilise nitrogen during the first few seasons of growth.

3   DISCUSSION

The results of the simulations described in the previous sections indicate the effects of leaf daily mass growth rate and leaf potential length have distinct effects on the growth of individual clones.

Leaf daily mass growth rate

Leaf daily mass growth rate affects total internal resource demands for growth placed by individual tillers. Increased leaf mass growth rate increases the daily demands of individual tillers. This in turn has two effects. It reduces the number of tiller recruitment events and increases the rate at which disproportionate resource allocation removes less efficient objects from each ramet group. These effects are shown by the early growth behaviour. Clones with larger mass tillers recruited less tillers during the first season of growth than clones with smaller mass tillers, even though the clones with larger tillers actually produced more biomass during the season. Once resources became limiting to growth during the second growing season, relatively more objects were terminated on clones with larger tillers than clones with smaller tillers. This corroborates evidence that there is an inverse relationship between the potential size of tillers of individual species and their ability to recruit secondary tillers (Tomlinson & O'Connor 2005).

Increased leaf daily mass growth rate appeared to increase resource capture abilities. This was shown by the clones which had identical leaf potential lengths but different leaf thicknesses, which affected the daily resource demands placed by each tiller on each clone. The clone with thinnest leaves accumulated less nitrogen annually than the other clones even though it maintained more live tillers, because it took longer to overcome carbohydrate limitation during spring regrowth and so allocated less resources to root growth at this time and hence was more restricted in its ability to capture soil nitrogen than the other clones.

Leaf daily mass growth rate determined potential leaf mass and hence potential tiller mass, which in turn determined the size of the tiller population maintained by the clone in

response to captured resources. Clones with tillers that had smaller potential mass leaves always maintained larger populations of live tillers than clones with larger potential mass leaves. Clonal internode mass was positively correlated with live tiller number, because internode mass on any given tiller does not die until after flowering is completed on that tiller. As internode mass was not adjusted for the height or the mass of the tiller, this provides a partial explanation for why clones with smaller potential mass leaves had greater biomass at the start of each spring. Consequently clones with smaller tillers are able to store more carbohydrate over winter, which may improve their ability to overcome the spring carbohydrate restrictions in closed swards.

Leaf potential length

The largest differences in nitrogen accumulation and growth productivity of clones were caused by differences in tiller potential height, as indicated by the behaviour of the set of clones with equal potential tiller masses but different leaf potential lengths. Clones with tillers that were short and fat accumulated much more nitrogen from the environment and produced more biomass than clones with tillers that were tall and thin. Consequently the former were able to support a larger number of tillers and greater biomass than the latter. This result is also supported by the first set of clones with different heights and different masses, where the clones with shorter, smaller tillers accumulated more nitrogen and produced more biomass annually than clones with taller, larger tillers.

The accumulated evidence suggests that there is a trade-off for bunchgrass species between the ability to capture soil nutrients and the ability to capture light that relates to the interactions between individual tiller structural properties, tiller mass growth rates and potential tiller height, and clonal structural properties, architecture and disproportionate resource allocation. Species that have greater leaf lengths will occupy vertical space more quickly and reach greater heights than tillers with shorter leaf lengths. However they trade this ability with the ability to recruit and maintain tillers and live biomass, which reduces their potential to occupy horizontal space when it is available and their ability to capture soil nitrogen when it is available. The simulations conducted here only considered a case where soil nitrogen was available for an extended period in spring. Under natural conditions, nitrogen pulse events would occur more frequently in response to wetting and drying cycles but for shorter periods (Birch 1958). This would probably further promote the growth of shorter-and-lighter tiller species over taller-and-heavier tiller species.

161

In addition, the clones with slower tiller mass growth rates grew more rapidly in the first few seasons of growth and were able to utilise the available resource space more quickly than clones with faster tiller mass growth rates because they were able to recruit and maintain more tillers during this period. This means that shorter-and-lighter tiller species may be able to pre-empt taller-and-heavier tiller species by securing a greater portion of the available nitrogen through more rapid expansion and acquisition of the resource. There are two consequences of this property. Firstly, if a new open horizontal space is colonised by equal numbers of seedlings of both lighter and heavier tiller species, and assuming that seed mass is equal across the species, then it is likely that at least in the first few seasons of growth, competitive dominance, as measured by nitrogen acquisition and horizontal space occupation, will be achieved by the species with lighter tillers. Secondly, if a disturbance opens up horizontal space among established bunchgrass clones, then the bunchgrass species with lighter tillers will spread more rapidly into the unoccupied space. In the long term it seems likely that as light competition between adjacent clones increases, then there may be a shift in the dominance of species from shorter tiller species to taller tiller species. However the rate at which this competitive replacement occurs may be slow, because the lighter tiller species has accumulated most of the nitrogen during the early phase of colonisation and continues to be a better collector of nitrogen through its growth strategy. This shift in dominance from shorter species to taller species in the absence of defoliation is well documented. In North America, long-term experiments indicate that the medium-height grass *Schizachyrium scoparium* gets replaced by the tall bunchgrass *Andropogon gerardii*, which Tilman (1988) argues is associated with the slow accumulation of nitrogen. In South Africa, the shorter *Themeda triandra* gets replaced by two taller species *Aristida junciformis* and *Eragrostis curvula* in non-defoliated swards in the Southern Tall Grassveld (Fynn *et al.* 2005a), however *Themeda triandra* remains dominant over these species if the treatments are regularly defoliated (also see Fynn *et al.* 2005b).

The behaviour demonstrated here supports Tilman (1988) in suggesting that, at least with respect to competing bunchgrass species, there is a trade-off between the ability to capture nitrogen and the ability to compete for light. The simulations indicate that if all other factors are equal, then clones of species with shorter-and-lighter tillers will colonise open space more quickly and collect nitrogen more quickly than species with taller-and-heavier tillers, because of demographic processes that change the populations maintained by each species. Clones of species with lighter tillers maintain a larger population of tillers than clones of species with heavier tillers, which allows the former to utilise soil nitrogen pulses

more effectively than the latter. This trade-off provides a mechanism that explains why inherently slower-growing species (lighter, shorter tiller species) can exceed growth rates achieved by inherently faster-growing species (heavier, taller tiller species) when nitrogen supply is not continuous, as recorded by Campbell & Grime (1989).

The evidence provided here contradicts the argument of Grime (1979) that the species competitive rankings remain constant across environments and therefore the potentially faster-growing species should always grow more quickly and be competitively dominant over the potentially slower-growing species in the absence of disturbance. As pointed out in the introduction, one problem which may be responsible for the persistence of this paradigm is that the definition of potentially faster-growing and potentially slower-growing plants is not sufficiently explicit. In this chapter I have provided a clear definition using the potential growth rates of individual organs of each species. Using this definition it becomes apparent that the growth potential of individual plants is temporally variable and depends on tiller population dynamics and temporal environmental resource availability. This in turn allows inherently slower-growing species to grow better in environments with variable and limited resources than inherently faster-growing species.

The behaviour demonstrated here arose from the architectural arrangement of bunchgrass clones, which consist of connected and disconnected tillers and ramets, sharing and competing for limited resources, and from the disproportionate allocation of resources between these structures, which increased the rate of dieback on potentially faster-growing clones and reduced their total productivity and ability to utilise the temporally-variable resource base. The simulation results obtained from the TILLERTREE model are at odds with results obtained from non-structural models that predict that faster-growing species will always be more productive (Van der Werf et al. 1993b). This evidence suggests that models of clonal growth must consider architecture, discrete-type behaviour and temporal shifts in resource availability in order to simulate the growth abilities of clonal plants under natural conditions appropriately. Only by this means can their true competitive abilities be assessed. Similarly the evidence suggests that pot-trial type studies of competition between inherently fast- and inherently slow-growing species have usually failed to pick up trade-offs in competitive ability because they supply nutrients to the plants continuously (e.g. Van der Werf et al. 1993a), and therefore fail to simulate the discontrnuous pulse manner in which soil nitrogen becomes available to plants growing in grasslands under natural conditions.

Chapter 10:   General Discussion

In order to understand how bunchgrasses achieve dominance over other growth forms and how they achieve dominance over one another in different environments, it is first necessary to develop a detailed understanding of how their growth strategy interacts with the resource limits of their environment. The aim of this thesis was to assess the consequences of interactions between architectural growth characteristics and disproportionate resource allocation in individual bunchgrass clones for their growth potential and ability to capture environmental resources. This was addressed by developing a simulation model, the TILLERTREE model, which appropriately captured the important components of the problem.

In this chapter I revisit the main objectives of this thesis and summarise the main results from the previous chapters in order to discuss their implications for current understanding and identify future directions for research.

1   CRITIQUE OF THE TILLERTREE MODEL

The first objective in this thesis was to construct a model that integrated architectural growth and resource capture and allocation in individual bunchgrasses. The TILLERTREE model is the first model of its kind that fully integrates architecturally-explicit simulation of clonal bunchgrasses and explicit resource capture and allocation of both nitrogen and carbohydrate. This means that clonal growth in the model is strictly limited by the internal resources available to the clonal ramet groups. Integration of architectural simulation and resource-limited growth has been achieved previously for simulations of individual non-clonal plants (e.g. Sequeira *et al.* 1991; Allen *et al.* 2005). A separate set of models have been designed to assess clonal growth architecture and horizontal spread (e.g. Oborny 1994; Piqueras & Klimeš 1998; Herben & Suzuki 2002). However, in most of these models, rules of resource acquisition and allocation are imposed over the plants rather than driven internally by the availability of resources. In addition these models ignore vertical characteristics of growth, which means that they are more suitable for assessing horizontal

spread of stoloniferous-type species and some rhizomatous species, than for bunchgrasses where vertical distribution of material is critical to growth dynamics. The latter is clearly demonstrated by the strong differences in growth potential achieved by clones with tall tillers and clones with short tillers (Chapter 9). This indicates that at least with respect to the growth of upright bunchgrasses, the TILLERTREE model shows clear advantages over existing non-vertically-explicit models.

The major weakness with the TILLERTREE model is that it is only 2-dimensional, being vertically explicit but not horizontally explicit. Therefore it cannot fully capture the horizontal spatial effects of clonal spread. Horizontal dynamics in bunchgrasses are certainly important, though for different reasons to the horizontal dynamics of stoloniferous plants. Stoloniferous plants expand internodes horizontally in order to seek and find soil resource patches in horizontal space (Oborny 1994), while bunchgrasses can only expand horizontally at the rate at which they can recruit new ramets (Briske & Demer 1998). Certain known spatial properties of bunchgrass tufts, such as hollow crown phenomenon and tuft fragmentation (Gatsuk et al. 1980) have not been explained satisfactorally (Briske & Demer 1998), although it is understood that the behaviour may result from the spatiotemporal availability of resources. It is probable that a 3-dimensional version of the TILLERTREE model will be able to demonstrate which processes control these phenomenona and what determines the rate at which these processes progress.

The next stage of development for the TILLERTREE is to expand it to a 3-dimensional configuration in order to assess horizontal effects in bunchgrass development and growth. Advanced 3-dimensional virtual plant models of trees have previously been constructed that generate highly realistic representations for computer graphics (Hallé, Oldeman & Tomlinson 1978; Borchet & Honda 1984; Prusinkiewicz & Lindenmayer 1990; Allen et al. 2005). The methods used for these models will be evaluated in order to extend the TILLERTREE model to the 3-dimensional format.

2 EFFECTS OF INTERACTIONS BETWEEN ARCHITECTURE AND RESOURCE ALLOCATION ON GROWTH AND RESOURCE CAPTURE IN INDIVIDUAL BUNCHGRASS CLONES

This thesis demonstrated that interactions between architecture and disproportionate resource allocation affect the ability of bunchgrass clones to capture environmental resources and the manner in which those resources are used. These properties were shown both with single-tiller simulations, in which disproportionate allocation between roots and shoots affected the ability of single-tiller ramets to overcome seasonal patterns of environmental resource availability (Chapters 6 and 7), and with multiple tiller simulations, in which it was demonstrated that disproportionate allocation among tillers on the same ramet and among ramets on the same ramet group affected both the ability of bunchgrass clones to capture seasonally variable resources, and seasonal growth characteristics (Chapters 8 and 9).

The single-tiller ramet simulations investigated how bunchgrass plants overcome seasonal effects in the environments they inhabit, which contain both growing and non-growing seasons. A critical problem is how to overcome light limitation when growing new photosynthetic surface in closed swards. This problem arises because of the architecture of bunchgrasses: they are composed of upright tillers that rapidly accumulate biomass, which in turn depletes light penetration through the overlying canopy. Bunchgrasses are generally poor at storing nutrients relative to other plant growth forms because they lack true storage organs and have poor storage abilities in exiting live tissues (Danckwerts 1984; Farrar & Williams 1991; Briske & Derner 1998). Therefore they cannot rely on stored reserves alone to provide sufficient resources for regrowth to overcome the light limitation. The simulations conducted here suggest that plants overcome the resource bottleneck through the combined effects of structural adaptations (etiolation, non-linear blade mass growth, residual live photosynthetic surface) and disproportionate resource allocation between shoots and roots (Chapters 6 and 7). These combined adaptations allow bunchgrass plants to overcome the light limitation through increased temporal resource efficiency that promotes shoot growth in early spring, which subsequently improves the carbohydrate supply for root growth.

The multiple tiller simulations demonstrated that significant interactions arise between the discrete object population architecture of bunchgrasses and the nature of resource allocation among objects (Chapter 8). Individual bunchgrass clones consist of

167

disconnected ramet groups that each consist of connected ramets and tillers. The live number of these objects determines the rate at which a bunchgrass clone can grow at any given time and also the total resource demand placed by those objects at any given time. It has been proposed that intra-clonal resource competition represents a mechanism for optimizing clonal resource allocation (Sachs *et al.* 1993). The level of disproportionate allocation determines the rate at which resources get allocated away from less efficient objects towards more efficient objects. Logically this will increase the performance of more efficient tillers and drive less efficient tillers towards termination. This reduces the tiller population size and increases the seasonal stability of the growth response of the bunchgrass clone. However the simulations indicate that increasing the rate at which disproportionate allocation occurs between objects on individual clones reduces their ability to capture seasonally variable resources, particularly the most limiting soil nutrient, nitrogen. This effect arises because more-disproportionate clones have fewer tillers and therefore are capable of smaller total growth rates when resources are available than more-proportionate clones. This evidence suggests that clonal bunchgrasses make a trade-off between individual tiller growth and total clonal growth.

The evidence of a trade-off between individual tiller growth and clonal growth suggests a fundamental difference in the allocation strategies employed by r-strategist and K-strategist plants in general (MacArthur & Wilson 1967). The r-strategists may favour more proportionate resource allocation in order to ensure maximum seed production, because they increase in non-competitive environments where quantity of growth and resource capture is more important than individual shoot performance. The K-strategists may favour more disproportionate resource allocation because this improves the growth of individual shoots (quality) in competitive environments, but at the expense of total seed production. It may also favour the growth of large individual seeds because there is less competition across the plant for resources. The evidence of a trade-off between individual tiller growth and clonal growth also suggests that different types of bunchgrasses may employ different levels of disproportionate allocation based on their life strategy. Short-lived annuals may favour more proportionate allocation that promotes maximum tiller production and growth in order to increase total seed production (Beard *et al.* 1978; Young *et al.* 1987), while long-lived perennials may favour more disproportionate allocation in order to promote individual tiller growth and individual seed size in light-limited grasslands (Westoby *et al.* 1996). However disproportionate allocation may also be used to promote seed size in nutrient-poor environments.

In Chapter 9 this trade-off was explored further by examining the effects of tiller height, tiller size and daily growth rates using moderately disproportionate allocation. These simulations demonstrated that clonal resource capture was inversely related to individual tiller height. As tiller height appears to be a strongly associated with competitive dominance among bunchgrasses growing in closed swards (Fynn *et al.* 2005a; Tomlinson & O'Connor 2005), this suggests that there may be a trade-off in bunchgrass species between ability to compete for light and the ability to compete for nitrogen. Consequently the simulation results support Tilman (1988) in asserting that there is a trade-off in competitive strategy for the two nutrients, at least with respect to bunchgrass species. However the simulations demonstrated that this trade-off arises in clonal bunchgrasses because of interactions between architectural tiller population dynamics, resource allocation and temporally variable environmental resource availability alone, and therefore avoided the controversial physiological arguments of Tilman that species which are superior competitors for nitrogen are able to extract the resource to lower levels from the soil than other species (Grime 2001). A further criticism of Tilman's (1988) R* theory is that it was mathematically formulated using diffusion-type models that assume progressive shifts in resource availability in response to growth and dieback, and ignore rapid temporal shifts in environmental resource availability. The evidence from the simulations conducted here is that the shift in competitive ability arises precisely because of interactions between temporal shifts in resource availability and plant architectural and allocation properties.

This demonstrated trade-off provides a mechanism that explains why inherently slower-growing species (lighter, shorter tiller species) can exceed growth rates achieved by inherently faster-growing species (heavier, taller tiller species), in contrast to the arguments of Grime (1979) that competitive rankings of species should remain the same across nutrient gradients in the absence of disturbance. The simulations demonstrated that the result is caused by interactions between the population architecture of bunchgrass clones and disproportionate resource allocation between connected objects. These simulation results obtained from the TILLERTREE model are at odds with results obtained from non-structural models that predict that faster-growing species will always win competition (e.g. Van der Werf et al. 1993b). This evidence suggests that models of clonal growth must consider architecture, discrete-type population behaviour and temporal shifts in environmental resource availability in order to define the growth abilities of clonal plants appropriately. Only by this means can their true competitive abilities be assessed. However, it should be remembered that none of the simulations conducted in this thesis involved

direct competition experiments, in which different clones are 'grown' alongside one another to determine which obtains the competitive advantage. Therefore the conclusions reached here still require verification from such 'direct competition' experiments. These will be investigated with the TILLERTREE model in subsequent research.

Two related topics that were directly connected to clonal architecture were clonal disintegration of bunchgrasses and the resources governing secondary tiller recruitment. These were simulated in the light of information gleaned from proportionate and disproportionate resource allocation across the tiller populations (Chapter 8). The simulations demonstrated that clonal disintegration increased clonal growth stability and survival prospects and increased the seasonal productivity of bunchgrass clones, providing conclusive evidence that disintegration is beneficial to bunchgrass clones (Kelly 1995) because it improves temporal resource efficiency by reducing the amount of resource sharing between productive and non-productive tillers during resource bottleneck periods.

The simulations on resource rules governing tiller recruitment demonstrated that rules for both carbohydrate and nitrogen requirements were necessary to ensure appropriate recruitment in response to restrictions on the availability of either resource in order to reduce wastage during critical periods and thereby improve total growth. This suggests that responsiveness to both signals improves the growth potential of the bunchgrass clone thereby improving its competitiveness, which provides support to the integrated model of control over tiller recruitment proposed by Tomlinson & O'Connor (2004).

In summary, the simulations conducted in this thesis provide convincing evidence that interactions between architecture and resource allocation affect growth of clonal bunchgrasses, and are necessary to describe certain types of behaviour exhibited by higher plants (Herben & Suzuki 2002). These interactions between architecture and resource allocation have been considered before with respect to stoloniferous/ rhizomatous species (e.g. Oborny 1994; Herben & Suzuki 2002), and these have demonstrated spatial movements in response to spatial resource availability. However these models impose external, non-mechanistic rules on growth behaviour and they focus on rules of spread, rather than allowing simulated plants to respond to environmental resources through internally-directed resource allocation alone. Population architecture and disproportionate resource allocation need to be assessed in other clonal and non-clonal plants to determine their relative importance to other growth forms (Woodward 1987). As all higher plants are composed of phytomers and tiller shoots, the design of the TILLERTREE model is

sufficiently robust that it can be used to simulate other growth forms, making it a suitable tool to compare the behaviour exhibited across types.

3   HYPOTHESIS FOR THE DISTRIBUTION OF PERENNIAL BUNCHGRASSES BY HEIGHT ALONG SOIL NITROGEN GRADIENTS

This thesis demonstrated that the architecture of bunchgrass clones has a significant effect on their growth and their ability to capture environmental resources in response to temporal environmental resource dynamics. This effect arises from the expression of the dual architectural properties of discrete growth processes (phytomer recruitment, tiller recruitment, tiller death) that determine the rate at which clones can grow in response to dynamic environmental resources, and discrete object population dynamics that affect the efficiency of temporal resource allocation.

In particular, it was demonstrated that shorter tiller bunchgrass clones were better accumulators of nitrogen and maintained more live tillers than taller tiller clones because of the population dynamics that arose in response to temporal shifts in environmental nitrogen availability. This suggests a competitive trade-off between the ability to compete for nitrogen (shorter species are better) and the ability to compete for light (taller species are better). As total annual growth is most limited by soil nitrogen and the level of light restriction depends on the amount of biomass, this suggests that competition for the two resources may cause bunchgrass species to be distributed by height in response to nitrogen productivity of the local environment.

The trade-off associated with tiller height may plausibly provide an explanation for the distribution of perennial bunchgrasses across both local environments and larger landscapes, based on the soil nitrogen productivity of each site. Figure 10.1 provides a schematic representation for the distribution of bunchgrass species in non-arid environments in response to the nitrogen productivity of the site, with tiller height increasing with increasing soil nitrogen productivity.

A second, theoretical property demonstrated in this thesis, the level of disproportionate allocation, which causes a trade-off between individual tiller growth and total clonal growth may be associated with bunchgrasses of different heights. As light competition occurs at both moderate and high nitrogen availability, shoot growth efficiency is important to ensure that clones remain competitive across the temporal shifts in resource

Competition for N	Competition for light and N	
Minimal light competition	N competition stronger	Light competition stronger
Short tiller species	Medium-height tiller species	Tall tiller species
Proportionate allocation	Disproportionate allocation	Disproportionate allocation

Low	Moderate	High

Nitrogen productivity (g N yr^{-1})

Figure 10.1 Proposed effect of environmental nitrogen productivity on the distribution of perennial bunchgrass species.

availability. Therefore disproportionate allocation is likely to be a characteristic of these species that ensures better growth of fewer tillers which improves their competitiveness in the light-limited conditions. At low nitrogen productivity, there is insufficient growth activity to induce severe light competition among neighbours, so clonal dominance is based mainly on competition for nitrogen. Therefore clones allocate proportionately in order to maximise clonal growth. In addition tillers are short in order to maximise live tiller number and hence live biomass maintained over winter. The combination of these two properties ensures maximal growth rates during favourable growth conditions and hence greatest potential nitrogen accumulation by the clone.

The change in competitive advantage in response to competition for two resources agrees with the predictions of Tilman's R* theory (Tilman 1988), but the prediction is based purely on the effects of interactions between architecture and resource allocation, and avoids the controversial physiological aspects of Tilman's R* models on physiological aspects. The trade-off in competitive ability for light and nitrogen supports the leaf-height-seed (LHS) scheme of plant ecology strategies proposed by Westoby (1998), which recognises trade-offs in growth traits. However, where Westoby emphasises that height causes substantial differences in stem growth requirements of species from different growth forms (e.g. bunchgrasses versus trees), the present proposal recognises that the same trade-offs are made by species in the same growth form. The schema focuses on the distribution of perennial bunchgrasses in competitive environments, where plants increase at the expense of their neighbours through superior ability to capture the most liming resource. It avoids non-competitive environments where rules of growth may be quite different (Grime 1977). The schema also ignores the effect of disturbance on species distributions, which may add to the complexity of the plant distributions in any given environment (Lauenroth & Aguilera 1998; Grime 2001).

The schema is given credence from fertilisation experiments and the natural distributions of bunchgrass species. Composition data collected from a 50-year-old fertilisation trial in the Southern Tall Grassveld (Acocks 1953), of different levels and combinations of annual nitrogen and phosphorous application, indicated that medium-height species dominated the least fertile treatments (*Themeda triandra*, *Tristachya leucothrix*, *Setaria nigrirostris*) while taller species dominated more fertile treatments (*Eragrostis curvula*, *Panicum maximum*) (Fynn & O'Connor 2005). Notably this experiment also demonstrated separation of the tall species on the basis of phosphorous application,

indicating that phosphorous is also important to competition between bunchgrass species (Newsham & Watkinson 1998).

In North America the relationship between plant height and nitrogen has been noted by Tilman (1988). A field trial of different nitrogen applications at Cedar Creek demonstrated that short and medium-height bunchgrass species achieved peak abundance on low and intermediate nitrogen treatments (*Schizachyrium scoparium, Poa pratensis*) while tall species (*Agropyron repens*) achieved peak abundance on high nitrogen treatments. Tilman (1988) further argued that the successional replacement of *Schizachyrium scoparium* by the tall bunchgrass *Andropogon gerardii* is associated with the slow accumulation of nitrogen. He suggested that this replacement is based on differences in the root-to-shoot allocation. However it can be explained by the population dynamics associated with bunchgrass tiller height demonstrated in this thesis, because *Andropogon gerardii* is a substantially taller species than *Schizachyrium scoparium*.

Distribution by tiller height in response to soil nitrogen productivity may provide evidence for the distribution of ecotypes of *Themeda triandra* (Chippindall 1955). Downing & Groves (1985) collected four ecotypes of *Themeda triandra* from different altitudes (150 – 2400 m above sea level) across KwaZulu-Natal, in order to test whether the species' growth patterns were sensitive to temperature and thereby provide an explanation for their altitudinal distribution. They grew all four ecotypes in phytotrons at all four temperature ranges associated with each altitudinal environment, but found only limited differences across the ecotypes, indicating that the ecotypes had not evolved for the temperature regimes at each site. However the data collected by Downing & Groves (1985) did indicate that the alpine ecotype from the KwaZulu-Natal Drakensberg was shorter than the other three, followed by the two ecotypes from intermediate altitudes and finally the subtropical ecotype was the tallest of the four. One of the intermediate ecotypes used is a medium height variety from the Southern Tall Grassveld. Carbutt (2004) has since shown that nitrogen mineralization above 1800 m altitude in the KwaZulu-Natal Drakensberg is an order of magnitude less than from soil samples in the Southern Tall Grassveld. Carbutt (2004) proposed that the low nitrogen mineralization rates in the Drakensberg above 1800 m explains the prominence of Cape elements, which are adapted to low nutrient conditions, in that system. However it also provides support for the distribution of *Themeda triandra* ecotypes by height in response to soil nitrogen productivity because shorter ecotypes are better accumulators of nitrogen, as demonstrated by the simulation results in this thesis.

173

The simulations conducted in this thesis provide only limited evidence for a hypothesis for the distribution of species by height and level of disproportionate resource allocation. Critically, multiple-species simulations are required to confirm that the purported trade-off made by clonal bunchgrass species between the ability to capture nitrogen and the ability to compete for light, translates into real changes in competitive advantage across a gradient of nitrogen availability. Two-clone simulations (in which each clone represents an end of the trade-off spectrum) conducted at a series of levels of nitrogen availability will be sufficient to test this effect.

4   FUTURE RESEARCH DIRECTIONS

The simulations conducted in this thesis focussed on the growth of individual tillers and individual clones in order to explore the consequences of interactions between architecture and disproportionate resource allocation in bunchgrasses for their behaviour and limits of growth. The thesis only used one species, *Themeda triandra*, because this meant that the effects of architectural properties could be considered directly, while ignoring additional species-specific traits that would have complicated the behaviour. This approach has provided a strong foundation from which we may proceed to assess the effects of other organ-level properties on individual clonal growth and how these increase or decrease the ability of bunchgrass clones to utilise resources and survive different resource environments.

There are numerous differences between bunchgrass species beyond the size of individual organs and organ growth rates. These could cause substantial changes to their competitive abilities in humid grassland environments. For example, timing of sexual reproduction differs among species (Howe 1994; Appendix A1). Some species are able to recruit secondary tillers on expanded culms, while others are not (Appendix A1). Some species have photosynthetic stems, while others do not. Both of the latter may allow particular species to overcome photosynthetic deficits that occur at certain times of the year. Therefore it is necessary to incorporate these adaptations into simulations of clones of the different species in order to assess how they affect seasonal population processes, productivity and resource capture. This accumulated information will help us to identify further trade-offs that set up changes in competitive advantage across environmental gradients (Tilman 1988) and properties that provide explicit growth advantage to individual

bunchgrass species. These properties will be tested in multiple-tiller simulations as well to verify the competition effects. All of the above work will aid our understanding of how bunchgrasses respond to environmental limitations and thence what determines competitive advantage in different resource environments.

In this regard, effects of defoliation on individual bunchgrass clones will be explored. The model may potentially provide some clarity on the continued debate over the complex and sometimes apparently contradictory growth responses exhibited by bunchgrasses to defoliation (Ferraro & Oesterheld 2002), which probably relate to resource availability and the intensity of defoliation. A century of empirical evidence indicates that defoliation regimes have a significant role in determining compositional dominance in grasslands (e.g. Glover & van Rensberg 1938; Everson & Tainton 1984; Belsky 1992; Collins et al. 1998), which provides concrete evidence for trade-offs in growth strategies. The hypothesis for the distribution of bunchgrass species in response to nitrogen availability given in the previous section ignores the effect of defoliation regime, which may modify the competitive dominance hierarchy of the species. Therefore it is necessary to explore the effects of defoliation on the relative growth of different bunchgrasses. By this means it will be possible to assess how defoliation modifies the bunchgrass distribution schema provided in the previous section. Concurrent empirical research on the growth of a number of bunchgrass species in the Southern Tall Grassveld and the effects of nutrition and non-selective defoliation on shifts in compositional dominance among these species (Fynn et al. 2005a; Fynn & O'Connor 2005) provides the opportunity to compare this empirical data with the behaviour of the bunchgrass species as simulated by the TILLERTREE model.

5 CONCLUSION

This thesis has demonstrated that the architecture of clonal bunchgrasses constrains their growth behaviour and ability to utilise environmental resources. Disproportionate allocation between live objects at a number of hierarchical levels modifies the growth behaviour of bunchgrasses, allowing them to overcome critical resource bottlenecks and creating trade-offs in bunchgrass growth strategy. The level of disproportionate allocation between shoot structures leads to trade-offs between individual tiller growth and clonal growth, demonstrating structural growth properties that are remarkably similar to those employed by K-strategist and r-strategist plants in general, suggesting a fundamental difference in the allocation procedure employed by each strategy. The trade-off between individual tiller performance and total clonal growth also suggests that different bunchgrasses may apply different levels of disproportionate allocation according both to their life-strategy (annual versus perennial) and the level of resource limitation (light and/or soil nutrients) in the environments they inhabit. Changes to structural organ growth rates in combination with disproportionate resource allocation lead to further trade-offs in bunchgrasses between ability to compete for light and ability to compete for soil nutrients. The combined evidence has paved the way for a simple theory on the distribution of bunchgrass species in humid environments based on soil nitrogen productivity.

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184

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APPENDIX A1:

Phenotypic Growth and Resource Allocation of
Two Bunchgrass Species

ABSTRACT

Compositional shifts of bunchgrass species in the Southern Tall Grassveld in response to different combinations of non-selective mowing and burning appear to reflect differences in growth strategy among species, but there are few studies of South African grasses designed to test this. A descriptive study was undertaken both to observe how different species allocated resources in response to different defoliation treatments imposed at the start of spring, as it was thought that these responses might be critical for an understanding of tiller dynamics and compositional change in bunch grasslands. The study recorded the reproductive growth response of two spring-flowering species, *Themeda triandra* and *Eragrostis curvula*, subjected to three defoliation treatments: no defoliation (No Mow), defoliation during the previous summer (Summer Mow), and defoliation in early spring (Early Spring Mow). Plant growth response was separated into primary growth, measured as individual organ extension on individual phytomers, and secondary growth, measured as the number of secondary tillers recruited per live primary tiller. Phytomer growth depended on treatment and species. For either species, organ extension was greater for the No Mow treatment than for either of the two defoliated treatments. Tillers of *E. curvula* were substantially larger and grew faster than *T. triandra* tillers. In addition, apical meristems of *E. curvula* remained close to the ground until flowering. These combined differences are consistent with *E. curvula* being able to outcompete *T. triandra* in less-frequently defoliated swards. Secondary tiller recruitment was significantly related to defoliation treatment and species. Tiller recruitment was substantially lower on the No Mow treatment than for the two defoliation treatments, and tiller recruitment was greater for *T. triandra* plants than for

E. curvula plants. Accumulated blade length was negatively related to tiller recruitment. Results suggest that tiller recruitment was limited by nutrient demand of primary structures, a consequence of which is that *T. triandra* will recruit more tillers than *E. curvula* when defoliation opens up space, accounting for *T. triandra*'s dominance on more regularly defoliated treatments.

INTRODUCTION

Bunchgrasses are upright phalanx clonal plants that occur in a number of environments ranging from arid through to mesic conditions (Briske and Derner 1998). Bunchgrasses growing in humid environments largely ensure their survival by continued site occupation of existing clonal tufts (genets). This is achieved by balancing individual tiller performance with secondary tiller (ramet) recruitment (Olson and Richards 1988).

The Southern Tall Grassveld (Acocks 1953) is a multi-specific moist bunch grassland. Different combinations of non-selective mowing and burning can shift the composition of this grassland from dominance by one bunchgrass species to another (Fynn, Morris and Edwards 2005; Uys, Bond and Everson 2004). This effect is mediated by differences in growth strategy of the local species. Numerous ontogenetic studies have been conducted on local species which have given some insight into differences in seasonal growth pattern among considered species (e.g. Tainton and Booysen 1965; Rethman and Booysen 1967; Danckwerts *et al.* 1984). However few of these experiments have been designed to determine the non-seasonal growth traits accounting for different species responses to non-selective defoliation. By contrast, species traits relevant to the effects of selective grazing on composition are well-understood (e.g. Theron and Booysen 1966; O'Reagain and Mentis 1988).

In an effort to understand how species structural growth traits manifest themselves in population dynamics, the authors built an individual tiller-based model of grass growth that examines the effect of differences in resource allocation to primary structures (organs on existing tillers) and secondary growth (recruitment of new tillers). A descriptive study was undertaken to parameterise organ growth characteristics of different bunchgrass species for the model, from which key differences among species in patterns of resource allocation could be defined. This dynamic is considered critical for an understanding of tiller dynamics and compositional change in bunch grasslands.

Defoliation removes plant biomass, which changes the light regime in a plant stand. Light-grown plants possess the ability to perceive changes in the light environment and adapt their morphology quickly by moderating the extension of growing organs, which is known as the shade-avoidance syndrome (Casal and Smith 1989). Shoots of all higher plants are composed of phytomers that are recruited sequentially by the apical meristem. A phytomer is a plant growth unit that contains a leaf blade and sheath, the sub-adjacent internode to the leaf, and an axial meristem on the node that joins the leaf to the internode (Etter 1951). Phytomers with non-expanded internodes are located near the soil surface and are therefore termed basal phytomers, while phytomers with expanded internodes form part of the reproductive culm and are therefore termed culm phytomers. Secondary tillers are recruited when phytomer axial meristems grow out on parent primary tillers. They are termed culm secondary tillers and basal secondary tillers depending on where they are recruited in line with the phytomer definitions above. Phytomer growth is directly responsive to changes in the light environment. A simple means of distinguishing ontogenetic and plastic responses to the defoliation environment may be achieved by observing the growth pattern of individual phytomers across time and across defoliation treatments. Phytomer organ responses of tufted grasses are most easily observed on reproductive-phase tillers when internodes also expand.

Two spring-flowering species were chosen for this study in order to determine if there were differences in primary plastic growth and secondary tiller recruitment across distinct ontogenetic growth patterns and whether there was a consistent response to non-selective defoliation treatment across species. These were *Themeda triandra* (Forssk.), a species capable of both basal and culm tiller recruitment (Tainton and Booysen 1965), and *Eragrostis curvula* (Nees), which can only recruit basal tillers (Gibbs-Russell *et al.* 1990). *Themeda triandra* is an important forage grass that is abundant under moderate, regular defoliation regimes (Everson and Tainton 1984; Danckwerts and Nel 1989; Hodgkinson *et al.* 1989; LeRoux 1989). The local variety of *Themeda triandra* flowers from September to December, depending on when the growing season begins. *Eragrostis curvula* is a less palatable but equally important grazing species that becomes abundant under lower frequency defoliation regimes than those suited to *T. triandra* (Fynn *et al.* 2005; Uys *et al.* 2004). *Eragrostis curvula* is known to flower from August to June (Gibbs-Russell *et al.* 1990), but most flowers are produced during early summer (Field-Dodgson 1976; Rethman and Beukes 1988). At Ukulinga, the two species reach reproductive maturity within a month of one another during early summer, which made them suitable for comparison.

The following questions were asked:

1. How is growth allocation on flowering tillers, both to primary structures and secondary tillers, distributed temporally during the reproductive phase in each of the species?

2. How do different defoliation treatments imposed at the start of spring regrowth affect the growth allocation of reproductive tillers to primary structures and secondary tiller recruitment in each of the two species?

3. Are there distinct growth characteristics that might explain why the species respond differently to different types of non-selective defoliation relative to one another?

MATERIALS AND METHODS

The fieldwork was conducted on the Burn-Mow Trial on the Grassland Plateau at Ukulinga Research Farm (29° 24' E, 30° 24' S) of the University of KwaZulu-Natal in Pietermaritzburg, South Africa, during the 2000/2001 growing season. The plateau has an average altitude of about 842 m. Mean annual precipitation is 694 mm. Summers are hot and humid and winters are mild and dry, with mean daily minimum and maximum temperatures of 18.1 °C and 26.4 °C in February and 8.8 °C and 20.6 °C in July respectively. Soils vary in depth from 5 cm to 60 cm, and are classified as Westleigh (plinthic paleustalf) and Mispah (lithic ustorthent) forms. The vegetation has been classified as Southern Tall Grassveld (Acocks 1953), which is a humid closed grassland dominated by tufted grass species. The growing period of grasses is controlled by temperature and soil moisture, and generally extends from September to May each season.

Investigation 1:

The effect of defoliation environment on primary growth allocation and secondary tiller recruitment

Three defoliation treatments were selected from the Burn-Mow Trial: *No Mow*: no defoliation after the mow on 4 May 1999; *Summer Mow*: mown during summer (14 December 1999 and 18 February 2000) of the previous growing season; *Early Spring Mow*: mown after first > 1 cm rainfall event in spring (21 September 2000) before growth commenced. The three treatments were perceived to represent different levels of biomass density in spring as a consequence of their defoliation regime. Each treatment plot was 13.7 m by 18.3 m. All treatments had been mown in the winter before the last growing season (4 May 1999). Mowing reduced aboveground phytomass to a height of about 80 mm depending on the evenness of the site. All cut material was removed from the site after the defoliation event.

None of the treatments removed the apical meristem of the primary tillers of either species marked during the trial, so apical dominance remained intact. Average total leaf area index (LAI) between tufts on each treatment was measured at the beginning and end of the experiment with a LAICOR-2000 sensor (LAICOR International Ltd, Vancouver, Canada). These indicate large differences in LAI across the treatments (Table 1). The No Mow treatment had an average disc meter height of 203.0 ± 8.22 mm (100 disc meter readings) prior to the start of spring regrowth based on the accumulation of live and dead material; disc meter heights on the other two treatments were both less than half this value (Dillon 1980).

During July and August 2000 prior to the experiment, no rain fell at Ukulinga and no grass shoot growth was observed during this period and consequently there was very little live photosynthetic material on tillers of the considered species on any of the treatments. Soil moisture was recharged by the first substantial spring rain event on 17 September 2000 (51 mm), which initiated spring regrowth. Plant sampling began on 13 October 2000 and was completed on 9 January 2001. Rooted grass plants, which may consist of multiple primary tillers growing off a single root system, were the sampling units. In order to avoid plant size effects caused by differences in the number of connected tillers, secondary tiller recruitment was measured as the number of tillers recruited per primary growing tiller initiated during the previous growing season. Secondary tillers were separated into culm secondary tillers and basal secondary tillers.

201

Table 1 Average total leaf area index (LAI) measured between tufts on three treatments on the Burn-Mow Trial at Ukulinga on the 30 October 2000. Leaf area index was measured with a LAICOR-2000 sensor. (The estimates were averaged from eleven readings on each treatment, where each measurement was taken by placing the LAICOR-2000 sensor on bare ground between neighbouring tufts. Variance of the samples was note recorded.)

Treatment	Start of Experiment	End of Experiment
No Mow	3.25	3.69
Summer Mow	1.43	2.60
Early Spring Mow	< 0.5*	1.61

* grass stubble was too short after the mow to obtain an accurate measurement

In order to determine the temporal distribution of primary tiller growth and secondary tiller recruitment, tillers were measured both by monitoring organ extension rates and tiller recruitment on permanently marked individuals, and organ growth on tillers collected from the site at sampling intervals of two to three weeks. Generally primary tillers of *E. curvula* and *T. triandra* both flower during the second spring, and very few tillers recruited at the start of spring flower that same spring (Field-Dodgson 1976). Therefore individual tillers were chosen on the basis that they appeared to be entering the flowering phase and had been recruited in the previous growing season, indicated by a raised meristem associated with old dead leaves and the presence of secondary tillers. A single reproductive tiller on fifteen independent tufts of each species were permanently marked on the No Mow treatment in order to record growth allocation and organ extension and senescence rates of the primary reproductive tillers, and recruitment and survival of secondary tillers initiated off the primary tillers in the non-defoliated sward. Growth allocation of primary tillers was measured in terms of organ lengths of blades, sheaths and internodes, which served as a surrogate measure for biomass. Blade maximum extension rate was calculated by averaging the blade maximum extension rate for each monitored tiller, which in turn was taken as the blade maximum extension rate across all phytomers measured on that tiller. Blade maximum senescence rate was calculated in a similar fashion.

For the destructive sampling, six rooted plants per species were randomly collected from other tufts on the No Mow treatment at the same time as the monitored tillers were measured. Lengths of blades, sheaths and internodes were measured on all phytomers that

had grown during the present growth season on the oldest living primary tiller. Lengths of each organ type on the chosen phytomers were summed for each primary tiller on each plant at each sampling to give a measure called 'accumulated organ length', which was used for comparing tiller growth allocation by organ type with respect to time. Data was collected beyond the peak of flowering.

Fifteen rooted plants of each species were collected off each treatment when the given species was at peak flowering on that treatment. For both species, flowering on the No Mow peaked in the last week of November, while flowering on the defoliated treatments peaked a week later. Each phytomer on each tiller that had developed after the winter rest was numbered to identify its position in the sequence of development. Blade, sheath and internode lengths were measured for each phytomer on the oldest flowering primary tiller as described previously. These were again summed to give accumulated organ lengths for the oldest flowering primary tiller. The number of secondary tillers that grew off each primary tiller were also recorded and separated into basal and culm tillers, further separated into live and dead categories.

The data was analysed using GenStat (5th edition) (Lawes Agricultural Trust 2000). The tiller recruitment data was log transformed ($y = \log (y + 1)$) to reduce variance. A two-way unbalanced analysis of variance (ANOVA) of total tiller recruitment per primary tiller against defoliation treatment and species and similar ANOVAs on organ lengths of individual phytomers were conducted. Following this, total tiller recruitment was regressed against accumulated blade length, accumulated sheath length and accumulated internode length of parent primary tillers using multiple linear regression with species treated as a block effect, after checking for collinearity. Backward selection was used to remove non-significant variables.

Investigation 2:

Species-specific mass estimates

Mass allocation to organ parts at flowering

Themeda triandra and *E. curvula* are both spring-flowering species. It is possible that their proportional allocation to stem, leaves and the inflorescence may be distinctive. Therefore total leaf mass was also measured for these two species. Material was collected for each species off the Early Spring Mow treatment during peak flowering (12/14/00 for *T. triandra* and *E. curvula*, and 03/13/01 for *A. junciformis*). Fifteen tillers of each species were oven-dried and weighed by organ type (leaves, stem, and inflorescence).

Specific leaf mass

Material for the specific leaf mass to length (g DM mm^{-1}) estimates was collected off the Early Spring Mow treatment on the 25 October 2000, when the leaves were still young but fully expanded. The intention was to avoid secondary compound deposits. Fifteen leaves of each species were selected randomly off tillers. Blade material was separated from sheath material. Each blade or sheath was passed though the planimeter to determine its surface area, then its length was measured, after which it was oven dried and weighed to determine the associated mass. A further sample of 15 leaves of each species was collected the following year on 13 November 2001. The results given below represent the sum of these two samples.

There is sufficient evidence to indicate that the relationship between organ extension and mass growth in a growing blade is sigmoidal (Rawson & Turner 1982). Therefore additional data was collected for the species *Themeda triandra* both to confirm the non-linear relationship and to get a lower estimate for the specific leaf mass of blades of *T. triandra* to be used in the model. Data was collected on 22 October 2003. Thirty five young leaves recruited during the same spring were used to obtain estimates for the minimum specific leaf mass to length.

204

Specific stem mass

Material for the specific stem mass to length ratio (g DM mm^{-1}) estimates was taken at the peak of flowering of the two species. Fifteen stems of each species were selected randomly off tillers taken from the Early Spring Mow treatment on the 13 November 2001. As culms taper towards the top, sections of the basal part of the stem and the upper part of the stem were measured in order to calculate the change in the specific stem mass to length ratio. This was necessary to the model in order to calculate the rates of internode mass gain after they have been extended.

RESULTS

Investigation 1: The effect of defoliation environment on primary growth allocation and secondary tiller recruitment

Temporal growth allocation in spring during the reproductive phase

Average spring secondary tiller recruitment and survival per primary tiller of each species on the No Mow treatment is presented in Figure 1. *Themeda triandra* recruited both culm and basal tillers, while *E. curvula* recruited only basal tillers. There was a strong switch from basal secondary tiller recruitment to culm secondary tiller recruitment of *Themeda triandra* tillers, which may simply reflect the fact that tillers are recruited close to the apical meristem. Spring recruitment off primary tillers growing under a closed sward was greater for *T. triandra* than for *E. curvula*, and most basal recruitment occurred during the early part of spring growth. Culm secondary tiller recruitment on *T. triandra* primary tillers increased further after the flowers had matured and the seeds had dehisced in mid-December. Secondary tiller recruitment on *E. curvula* appeared to be increasing linearly during the trial.

Mean maximum blade extension rate and senescence rate were both significantly faster on reproductive *E. curvula* tillers than on *T. triandra* tillers (Table 2). The accumulated organ lengths for phytomers that grew during the spring regrowth period through to flowering of each species indicate that individual reproductive *E. curvula* tillers were substantially larger than *T. triandra* tillers (Figure 2) and the rates of biomass
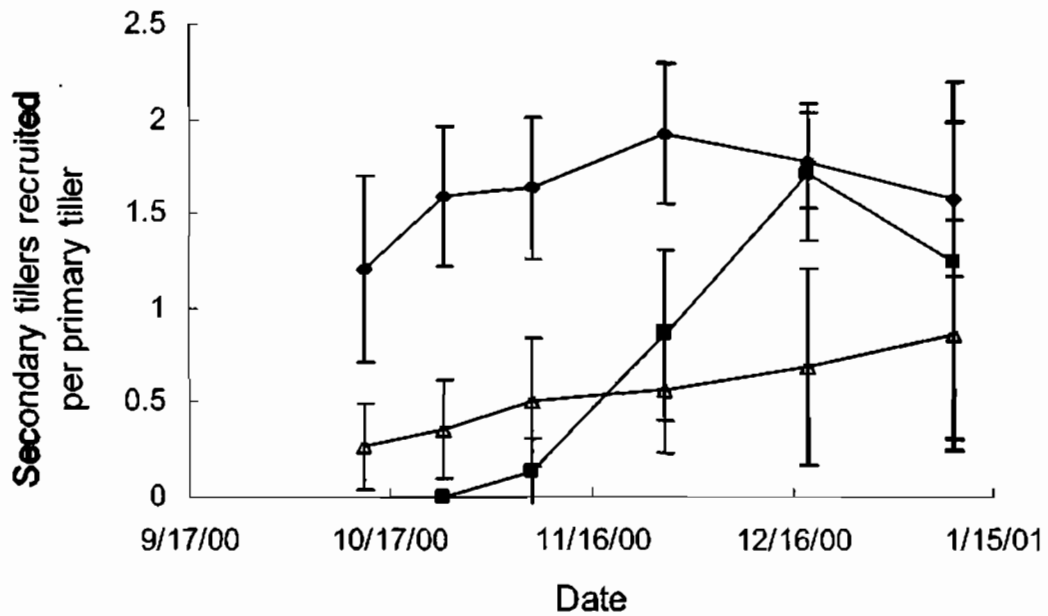
Figure 1 Average secondary tiller recruitment and survival per primary tiller on plants of *Themeda triandra* (♦ basal tillers, ■ culm tillers) and *Eragrostis curvula* (Δ basal tillers) monitored during the 2000/1 growing season on the No Mow treatment. Vertical bars represent 95 % confidence limits.

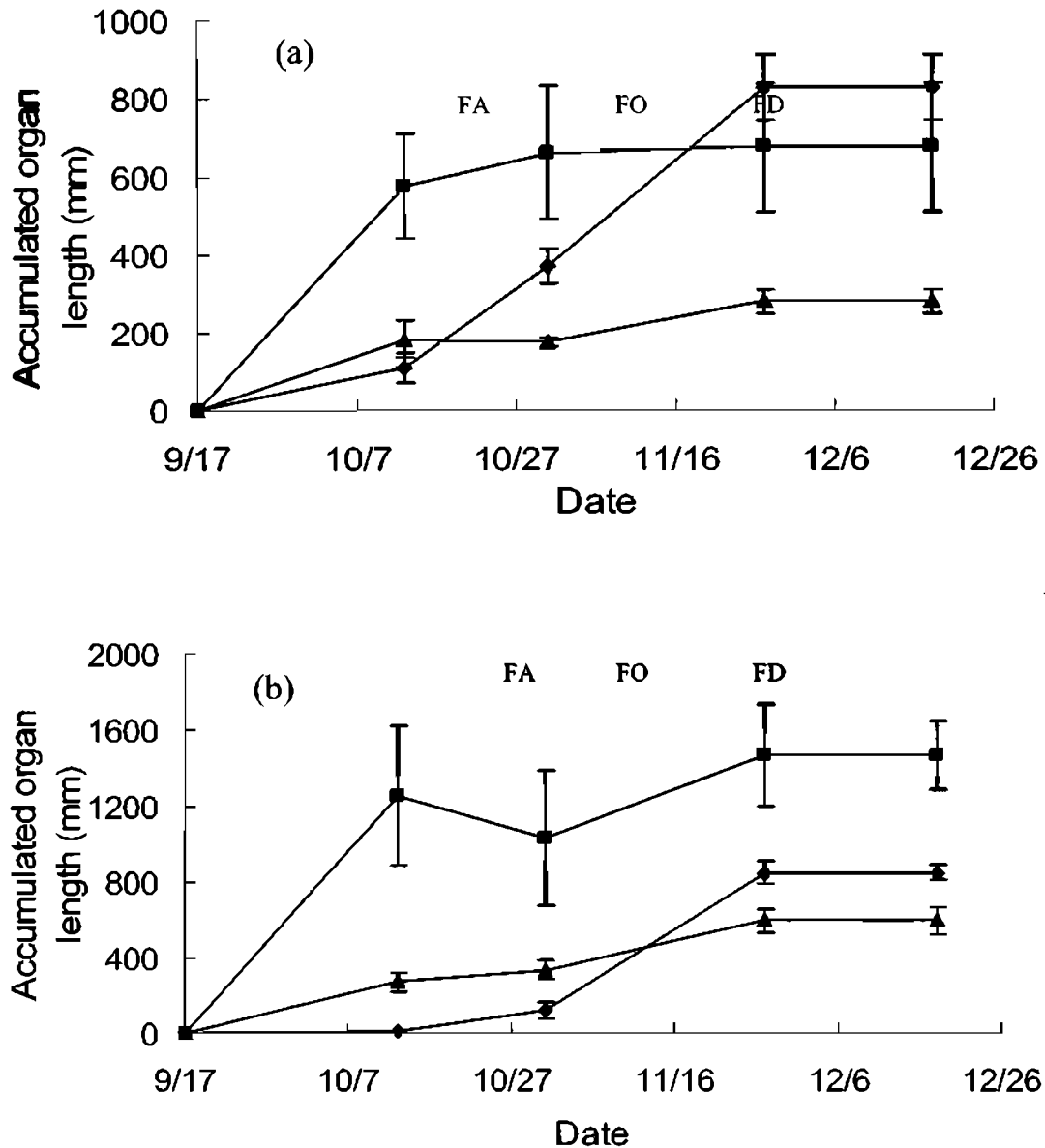**Figure 2** Accumulated organ lengths of phytomers that grew during the spring regrowth period on reproductive tillers collected from the 13 October until peak flowering on the No Mow treatment (▲ sheath, ■ blade, ◆ internode). a. *Themeda triandra*. b. *Eragrostis curvula*. (FA – flowers appear, FO – flowers open, FD – flowers dead.) Vertical bars represent 95 % confidence limits. Note the different scale for each species.

accumulation suggest that daily growth resource demands of *E. curvula* tillers were substantially greater than those for *T. triandra*. By the first sampling on 13 October most of the leaves of both *T. triandra* and *E. curvula* flowering tillers had already grown to almost full length within a month after the first substantial spring rainfall on 17 September. In contrast, the stems of both species had undergone only minor extension from their values prior to spring regrowth. Importantly the total length of internodes on phytomers recruited during the previous season indicated that apical meristems of *T. triandra* were already raised on average to 75.4 mm at the start of spring regrowth, whereas the same measure for *E. curvula* was only 6.6 mm, indicating that the latter species' apical meristem was much closer to the ground. Subsequent samples showed rapid elongation of the culms of both species (indicated by the accumulated internode length in Figure 2), where the culms of *T. triandra* started elongating sooner than those of *E. curvula*, but culms of the latter species elongated more rapidly. The temporal separation between leaf growth and stem growth suggests that tillers of both species construct photosynthetic organs first, in order to supply energy for culm expansion and inflorescence development. The peak of flowering was during the last week of November and the first week of December. By mid-December, most of the seeds of *T. triandra* had already fallen and seed of *E. curvula* had begun to fall.

Table 2 Mean maximum (± 95% confidence intervals) leaf blade extension and senescence rates (mm day^{-1}) for the two grass species collected off the Burn-Mow Trial at Ukulinga during spring/summer 2000

Themeda triandra	Blade extension rate	8.18 ± 0.93
	Blade dieback rate	-7.66 ± 1.70
Eragrostis curvula	Blade extension rate	17.40 ± 2.05
	Blade dieback rate	-14.69 ± 2.45

Average lengths of leaf blades, sheaths and internodes on consecutive phytomers and total culm lengths of primary tillers are presented for each species on each spring defoliation treatment at full flowering (Figures 3 and 4). Blade length best distinguished the treatments, followed by sheath length and then internode length. ANOVAs on individual phytomer organ lengths of each species for defoliation treatment (data not included) showed that all sheaths and blades of flowering-stage phytomers of *T. triandra* and *E. curvula* responded significantly to treatment, whereas the differences in internode length of some phytomers were non-significant. Tillers growing on the defoliated treatments always had shorter blade and sheath lengths than the No Mow treatment, suggesting that this response is light-mediated as leaves on tillers on the No Mow treatment were forced to grow through a taller dead sward during spring than tillers on the other treatments.

Internode length responses of the phytomers differed between *T. triandra* and *E. curvula*. In the case of *T. triandra*, internodes on earlier phytomers were longer on the No Mow than for the defoliated treatments, but the tillers taken from the Summer Mow had the longest internode for phytomer 5 and there were no significant differences for Phytomer 6. Similarly, internodes on early phytomers of *E. curvula* were longest for the No Mow, but in contrast to *T. triandra*, internodes on the last phytomer of *E. curvula* tillers were significantly different where tillers from both defoliated treatments were substantially larger than the No Mow. Consequently culm length was significantly different across treatments for both *T. triandra* and *E. curvula*, but the underlying response to treatments differed between the species.

Secondary tiller recruitment data for both species and treatments is presented in Table 3. Basal secondary tiller recruitment per primary tiller was greater on defoliated treatments than on the No Mow for both *T. triandra* and *E. curvula*. Basal secondary tiller recruitment by *T. triandra* tillers on the Early Spring Mow treatment was substantially greater than on either of the other treatments for this species, but this also had the lowest culm secondary tiller recruitment. Basal secondary tiller recruitment by *E. curvula* tillers on the two defoliation treatments was quite similar and substantially different from the No Mow treatment. *Themeda triandra* primary tillers consistently recruited more secondary tillers than *E. curvula* within each treatment during the trial. Mortality of *T. triandra* secondary tillers occurred on all treatments whereas mortality of recruited tillers of *E. curvula* was minimal during the experiment.

207

Figure 3   Average organ length data of flowering tillers of *Themeda triandra* across defoliation treatments (☐ No Mow, ■ Summer Mow, ▦ Early Spring Mow) collected at the peak of flowering (No Mow 27 November 2000, Summer Mow and Early Spring Mow 6 December 2000). Vertical bars represent 95 % confidence limits.
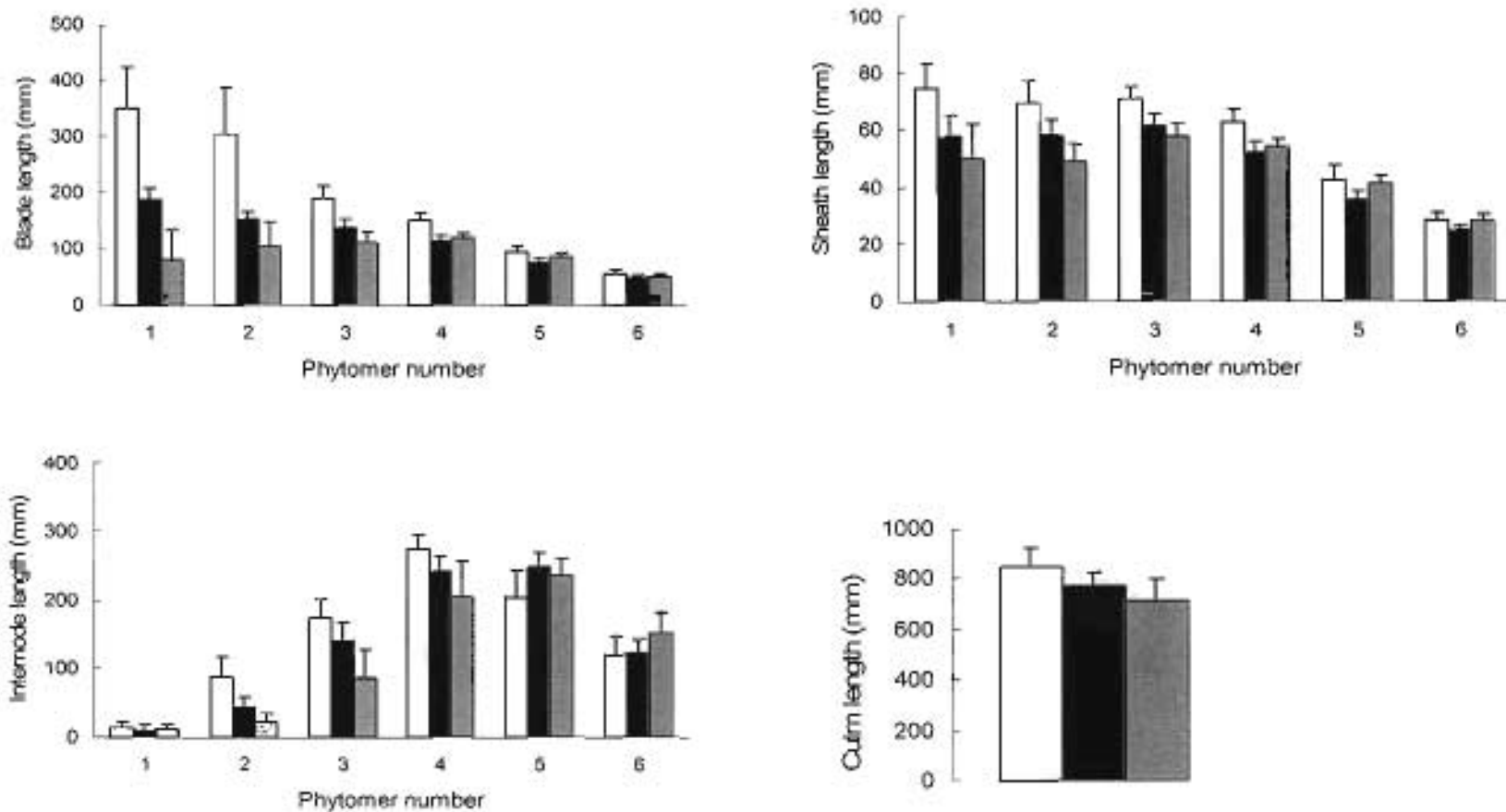
Figure 4 Average organ length data of flowering tillers of *Eragrostis curvula* across defoliation treatments (☐ No Mow, ■ Summer Mow, ☰ Early Spring Mow) collected at the peak of flowering (No Mow 27 November 2000, Summer Mow and Early Spring Mow 6 December 2000). Vertical bars represent 95 % confidence limits.
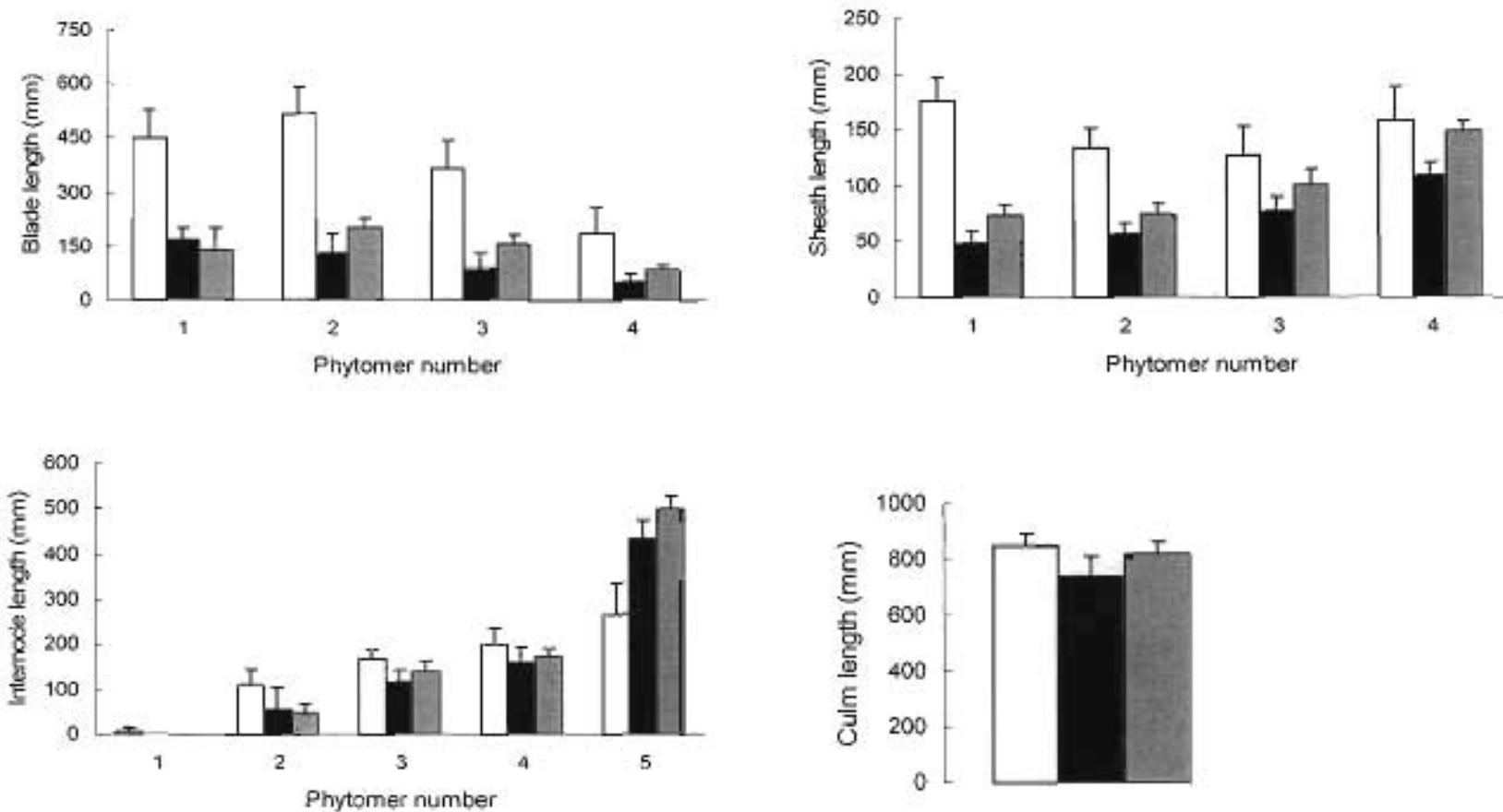
The ANOVA of log transformed total tiller recruitment per parent tiller (Table 4) indicated that secondary tiller recruitment was significantly different between species and treatments while their interaction was marginally non-significant. The most striking characteristic of the tiller recruitment data was its large variance even within species-treatment combinations. Regression analysis of tiller recruitment versus primary tiller growth with species treated as a block effect showed that tiller recruitment was significantly negatively related to accumulated blade length, but there was no relation with accumulated sheath length or accumulated internode length (Table 4). Species had as strong an effect as accumulated blade length. The regression was highly significant although the total variance accounted for was low.

Table 3   Average (± 95% confidence intervals) secondary tiller recruitment per primary tiller on reproductive tillers across defoliation treatments collected off the Burn-Mow Trial at Ukulinga during spring/summer 2000

Species	Treatment	Basal secondary tillers		Culm secondary tillers	
		Total	Dead	Total	Dead
Themeda	No Mow	1.07 ± 0.327	0.32 ± 0.184	1.20 ± 0.472	0.08 ± 0.119
triandra	Summer Mow	1.48 ± 0.426	0.51 ± 0.251	1.24 ± 0.259	0.04 ± 0.041
	Early Spring Mow	2.53 ± 0.987	0.31 ± 0.329	0.77 ± 0.499	0.03 ± 0.05
Eragrostis	No Mow	0.83 ± 0.428	0	-	-
curvula	Summer Mow	2.33 ± 1.093	0	-	-
	Early Spring Mow	2.20 ± 0.860	0.07 ± 0.131	-	-

Table 4 ANOVA and multiple regression of log spring secondary tiller recruitment per primary tiller across species and defoliation treatments for tiller data collected off the Burn-Mow Trial at Ukulinga (default species: *Eragrostis curvula*) during spring/summer 2000

Analysis of variance

Treatments	F	P	d.f.	c.v.%
			98	43.50
Treatment	8.78	<0.001		
Species	15.61	<0.001		
Species. Treatment	2.39	0.097		

Regression analysis

	F	P	d.f.	R^2
Regression	17.13	< 0.001	98	24.8%

Parameter	Estimate	t	P
Constant	0.4711	10.00	<0.001
Accumulated blade length	-0.000172	-3.71	<0.001
Species *Themeda triandra*	0.1709	4.18	<0.001

Investigation 2:   **Species-specific mass estimates**

Mass allocation to organ parts at flowering

Table 5 shows the mass estimates for organ parts of flowering tillers and the average ratio of inflorescence mass to stem mass for each species. The values of the average inflorescence to stem mass ratios (*T. triandra*: 0.149; *E. curvula*: 0.147) indicate that *T. triandra* and *E. curvula*, which have very similar mean ratio values. Both *T. triandra* and *E. curvula* allocate at least half of their shoot mass to stem construction, where *E. curvula* assigns the most to this function.

Table 5   Tiller organ mass data for the three considered species averaged from tiller data collected off the Early Spring Mow treatment (95 % CI included)

Species	Organ	Summed organ mass (g)	Proportional mass (g g^{-1})	Flower : stem ratio (g g^{-1})
Themeda triandra	Stem	0.305 ± 0.068	0.625 ± 0.029	
	Leaves	0.103 ± 0.019	0.225 ± 0.030	
	Inflorescence	0.072 ± 0.019	0.149 ± 0.030	
	Tiller	0.569 ± 0.093		0.149 ± 0.030
Eragrostis curvula	Stem	0.409 ± 0.067	0.528 ± 0.030	
	Leaves	0.253 ± 0.046	0.325 ± 0.019	
	Inflorescence	0.111 ± 0.024	0.147 ± 0.022	
	Tiller	0.773 ± 0.125		0.146 ± 0.022

Specific leaf mass

The specific leaf mass to area of *E. curvula* is almost double that of *T. triandra* (Table 6). Specific blade mass to area and specific sheath mass to area values of each species are similar to one another. Figure 5 shows the non-linear relationship between organ extension and mass growth of blades of T. triandra. The regression model suggests a lower estimate of about 0.00005 g DM mm^{-1} for *T. triandra*.

Table 6 Average estimates for specific leaf mass and maximum blade widths for the three grass species (95 % confidence intervals are included)

Species	Leaf organ	Specific mass to area ratio (g DM cm^{-2})	Specific mass to length ratio (g DM mm^{-1})
Themeda triandra	Blade	0.00405 ± 0.000291	0.000172 ± 0.0000155
	Sheath	0.00444 ± 0.000721	0.000198 ± 0.0000234
Eragrostis curvula	Blade	0.00739 ± 0.001299	0.000257 ± 0.0000363
	Sheath	0.00758 ± 0.001246	0.000240 ± 0.0000593

Specific stem mass

Table 7 shows estimates for the stem mass to length ratio (g DM mm^{-1}) and stem density (g DM mm^{-3}) of the two considered species. The estimates indicate that stem density is significantly different between the two species. There is also a large difference in the stem mass to length ratio between culm bases and culm tops, as anticipated. The daily stem mass gain fraction of each species was calculated using the exponential function, using the stem mass to length ratio of the base and top portions of each culm, and the time taken for the culm elevation period. The estimates obtained were: 0.0183 g g^{-1} DM day^{-1} for *T. triandra*; 0.0070 g g^{-1} DM day^{-1} for *E. curvula*.
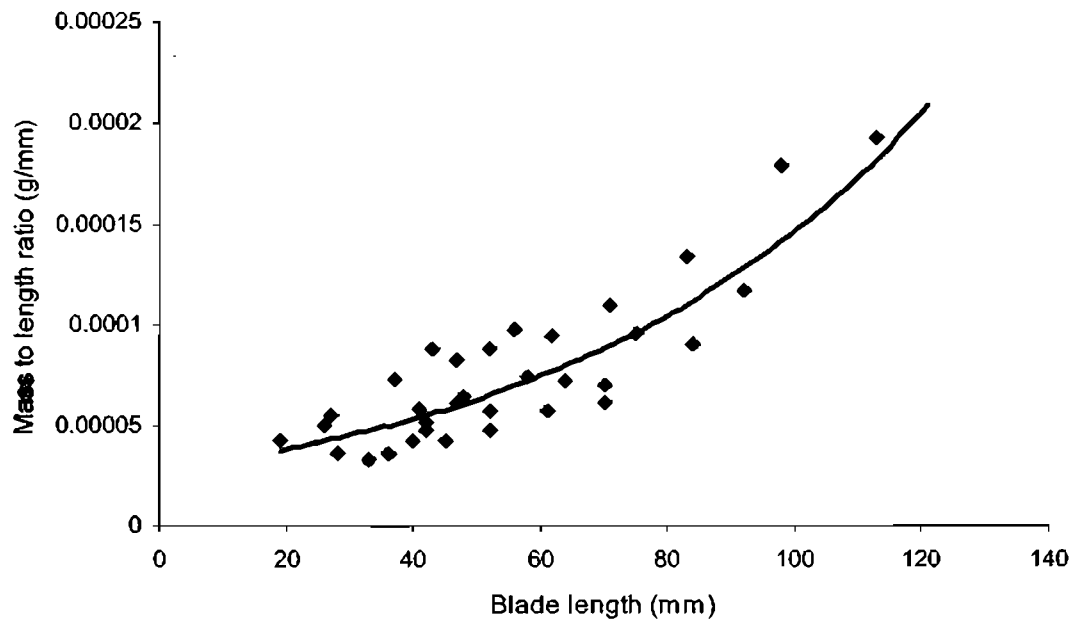
Figure 5   Relation between blade length and blade mass to length ratio (g DM mm^{-1}) on blades of *Themeda triandra* collected on 22 October 2003. Data points and regression model are shown (y = -0.00000008 x^2 - 0.0000006x + 0.000052; R^2 = 0.79).

Table 7   Estimates of stem density and mass to length ratios of the three considered species taken at the top and bottom of the stem (95 % confidence intervals are included)

Parameter	Species	Base	Top	Average
Stem mass to length	*Themeda triandra*	0.000891 ± 0.000123	0.000205 ± 0.0000225	0.000441 ± 0.000079
ratio (g DM mm⁻¹)	*Eragrostis curvula*	0.000541 ± 0.000061	0.000420 ± 0.0000339	0.000571 ± 0.000079
Stem density	*Themeda triandra*	0.000254 ± 0.000023	0.000324 ± 0.0000309	0.000289 ± 0.000022
(g DM mm⁻³)	*Eragrostis curvula*	0.000337 ± 0.000028	0.000431 ± 0.0000349	0.000387 ± 0.000021

DISCUSSION

The study demonstrated that both *Themeda triandra* and *Eragrostis curvula* possess ontogenetic traits that enable them to compete in tall grasslands. During the reproductive phase of growth, both species demonstrated temporal separation of leaf growth and stem growth. Leaf growth precedes stem growth, which allows the grasses to use stored reserves for constructing photosynthetic organs, as most leaf material was killed or senesced during winter. This separation presumably provides a two-fold benefit, by reducing the daily nutrient demand during the leaf growth phase and re-establishing photosynthetic material for subsequent carbohydrate requirements, which must be substantial during stem elevation and inflorescence growth. This separation would be particularly important when tillers are forced to grow through tall dead swards such as the No Mow treatment as substantial blade growth is required to penetrate the dead canopy to generate sufficient carbohydrate. Hence delayed stem elevation in spring is probably an adaptation to prevent resource restrictions during regrowth and not an adaptation to avoid grazing.

Stem elevation of *E. curvula* was delayed for longer than *T. triandra*, but the additional grazing-avoidance time this provides is probably coincidental. By contrast it is clear that blade expansion rates of *E. curvula* are substantially faster than *T. triandra*. In addition the blade and sheath lengths achieved by *E. curvula* are substantially longer than *T. triandra*, while total culm lengths are quite similar. This provides *E. curvula* with a two-fold competitive advantage in tall closed swards over *T. triandra*, as it is able to penetrate dead canopies more quickly in spring, which allows it to become photosynthetically self-

sufficient sooner during spring regrowth, and it is able to overshade *T. triandra* tillers in neighbour competition for light.

There is evidence that *T. triandra* is able to expand internodes marginally during the vegetative growth phase when growing in non-defoliated swards (Tainton and Booysen 1965), but this expansion is not substantial so the benefit is limited. In addition the early apical elevation makes the species more susceptible to defoliation. Apical decapitation prevents further leaf development on the stem and induces secondary tiller growth, forcing a slow recovery in photosynthetic surface as a result of meristematic limitation (Richards and Caldwell 1985). The evidence from this study indicates that *E. curvula* does not undergo apical elevation before reproductive growth. This suggests that *E curvula* is competitively advantaged over *T. triandra* under conditions of low to intermittent defoliation, which does not decapitate tillers of *E. curvula* but reduces the number of existing differentiable meristems available for regrowth on *T. triandra*. This provides an explanation of why *E. curvula* has increased in abundance in infrequently defoliated treatments of the Burn-Mow Trial at Ukulinga (Fynn *et al.* 2005) where both species occur.

Themeda triandra is partially able to compensate for slow growth rates and short leaves through its ability to recruit tillers along the culm which places culm tillers above the vegetative sward into direct solar irradiance, allowing the rooted plant to maintain high levels of photosynthesis. Longevity of culm tillers has not been researched, but personal observation suggests that they were capable of surviving at least one winter, although many die. It is probable that their position on the culm makes them susceptible to stem cavitation during water stress periods. Therefore culm tillering only provides *T. triandra* plants with a medium-term solution to light limitation in closed swards. Consequently if severe defoliation of the moribund material does not occur within two years then failure of culm tillers of *T. triandra* leads to light starvation and hence to death of entire clonal tufts (Everson 1985). This would further explain why the species declines in infrequently defoliated swards (Everson and Tainton 1984; LeRoux 1989; Fynn *et al.* 2005).

Both species demonstrate morphological plasticity in response to the applied defoliation regimes. Treatment had a significant effect on blade and sheath expansion of *T. triandra* and *E. curvula* tillers. Importantly though, the difference between the No Mow and the two defoliated treatments was far more substantial than the difference between the two defoliated treatments, although these were still significant. The treatment effect on internode length was not consistent and the length differences were far less substantial for most phytomers. This difference in the response of organs may in part be due to the

temporal separation of leaf and internode growth since it appears that photoreception occurs in young expanding leaves (Skinner and Simmons 1993). Hence internode growth may have been less affected by light conditions because almost all blades had completed expansion by the time internode elongation began.

The results indicate that secondary tiller recruitment during spring was significantly affected by species and defoliation regime, although the data variance was high. This variance in part may be ascribed to the small sample size and the discrete nature of the data. However, it also suggests that tiller recruitment is a secondary process that is only instituted if a set of conditions have been satisfied simultaneously in order to stimulate axial bud outgrowth, the means by which new tillers are recruited.

The negative relation between accumulated blade length and secondary tiller recruitment suggests that tiller recruitment is reduced when growth of primary structures is increased. Hence a grass plant's nutrient sink demand affects tiller recruitment, implying that nutrients are a requirement to stimulate tiller recruitment. This is the basic tenet of the Nutrition Hypothesis of lateral bud outgrowth (Trewavas 1981; Cline 1991). Corroborative evidence is provided by the significant difference in tiller recruitment between the two considered species. *Themeda triandra* initiated more secondary tillers than *E. curvula* at the start of the season. The greater secondary tiller recruitment rate of *T. triandra* was possibly a direct consequence of its slower accumulated organ expansion rate and hence smaller daily growth requirement relative to *E. curvula*. This could have reduced the sink demands for nutrients thereby releasing resources for allocation to secondary tillers. Additional mass measurements recorded for the two species (data not provided) indicated that all *E. curvula* organs were strictly heavier per unit length (g mm^{-1}) than their *T. triandra* equivalents, emphasising that daily resource demands for growth of primary structures of this species were substantially larger than for *T. triandra* tillers. This corroborates well with previous research comparing medium and short tufted graminoid species (McNaughton, Wallace and Coughenour 1983; Coughenour, McNaughton and Wallace 1985), which showed that tiller recruitment was substantially higher on the smaller species while estimated daily potential growth rates were higher on medium species (Coughenour, McNaughton and Wallace 1984).

The greater secondary tiller recruitment rate of *T. triandra* gives it the ability to rapidly colonise environments with a moderate defoliation regime, and probably accounts for its near dominance on moderately defoliated treatments on the Burn-Mow Trial (Fynn *et al.* 2005) and other grassland communities (Everson and Tainton 1984). Rapid tiller

214

recruitment under suitable environmental conditions potentially allows a grass genet to rapidly increase its photosynthetic surface, which provides resources for root growth and increased mineral absorption resulting in a positive feedback loop. Clearly, all other things being equal, when light is available, the bunchgrass species that can recruit the most tillers will take the most available space at the expense of its competitor species. Hence it seems likely that *T. triandra* maintains dominance over *E. curvula*, and probably over most other tufted species in the Southern Tall Grassveld, because it can tiller more rapidly after a defoliation event opens up light space for colonisation.

It is also possible that tiller recruitment could have been impacted by nutrient supply, particularly carbohydrate supply. The defoliation treatments may have substantially changed the amount of irradiance reaching blades during the early part of spring regrowth. This is suggested by the large difference in LAI between the three treatments. Light attenuation through a canopy is exponential (Beer's Law), so increased plant biomass would increase the level of light depletion. This probably reduced the photosynthetic efficiency of tillers growing on the No Mow treatment to a greater extent than for the two defoliation treatments, thereby reducing the nutrient supply to the plant and probably further reducing tiller recruitment. Unfortunately as this was an observational study designed to collect model data, no detailed measures of actual light irradiance or plant carbohydrate concentrations were obtained, so this argument is speculative. The combined evidence suggests that carbohydrate availability may have a strong regulatory role on secondary tiller recruitment of tufted grasses during spring and that nutrient supply-sink relations can explain the difference in tiller recruitment between species and across imposed defoliation regimes.

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APPENDIX A2:
Control of tiller recruitment in bunchgrasses: uniting physiology and ecology

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Summary

1. Tiller recruitment in clonal plants is a subset of the problem of lateral bud outgrowth in higher plants. This paper proposes that three competing hypotheses of lateral bud outgrowth, namely apical dominance, the nutrition hypothesis and photosensitivity to the red: far-red light ratio, may be linked in a logical fashion. In addition there is strong evidence to suggest that the balance among the three processes is both a function of the environment and plant form.

2. The evidence for each hypothesis is reviewed, following which we provide an integrated model that links the three hypotheses into a cohesive strategy. Subsequently we assess tiller recruitment by bunchgrasses in terms of the constraints of their functional growth form and their environment.

3. The integrated model maintains the accepted paradigm that actual bud release is hormonally controlled by the auxin:cytokinin ratio, although local nutrient concentrations may also be inhibitory. Importantly, each hormone is controlled by local signals in the shoots and roots respectively facilitating appropriate responses to environmental conditions. Auxin production and export from the shoots is moderated by phytochrome responses to red: far-red light ratios. Cytokinin production is mediated by root N concentration, which in turn is a function of N absorption from the soil and seasonal re-allocation of tissue N.

4. An examination of the growth form of bunchgrasses and the environment in which they are found emphasise that N has a strong mediatory role over tiller production which

allows the grass plant to respond appropriately to shifts in this limiting resource. This suggests that control of lateral bud outgrowth may have an evolutionary basis in resource competition.

Key words: graminoids, lateral bud outgrowth, nitrogen, plant growth, plant hormones

Introduction

Vegetative growth of tillers is a fundamental strategy employed by perennial, clonal grasses to ensure population persistence in their environments. Tillers are the replicated structures or ramets in clonal grasses, which may or may not be able to develop individual plant status based on genetic characteristics (e.g. aerial tillering) or environmental constraints (e.g. density effects). It is critical that some of the recruited tillers do root and become self-sustaining plants in order to maintain the clonal population once the parent tiller has died (Briske & Derner 1998). Tiller recruitment in wild populations is not randomly distributed through a growing season (Olson & Richards 1988) and the survival of these tiller recruitment cohorts is not equal (Butler & Briske 1988), but rather survivorship is closely related to the environmental setting into which new tillers are recruited (Tainton & Booysen 1965; Butler & Briske 1988). Clearly timing of tiller recruitments in a dynamic environment is critical for their survival as individual ramets and for the survival of the clonal genet.

A number of reviews have looked at the possible mechanisms by which lateral bud dormancy may be broken (e.g. Phillips 1975; Cline 1991; Cline 1994). Briske & Derner (1998) evaluated existing theories on the mechanisms that regulate tiller recruitment. They reduced the list to three: apical dominance, resource competition/ resource availability, and photosensitivity to the red:far red light ratio. Briske & Derner (1998) found inconsistencies with each mechanism and concluded that searching for a sole regulatory mechanism for ramet regulation may have limited success, as regulation by a single mechanism would potentially constrain morphological plasticity. They added that multi-variable models have received minimal research emphasis.

The aim of this paper is to unite the current theories on the mechanisms of lateral bud outgrowth into an integrated theory that provides an evolutionary sound model of secondary tiller recruitment in bunchgrasses. We begin by reviewing the three mechanisms in order to weigh up the evidence for each as Briske & Derner (1998) did previously. We

extend their analysis by evaluating the evidence for linkage among the three mechanisms in light of additional research that has accumulated both prior and subsequent to their review in order to propose an integrated, multi-variable model that links the three components in a logical fashion. Subsequently, we consider the theories in the light of the limitations imposed on tufted grasses by the consequences of their own growth form and by the environment in which they occur. Finally, we show that nitrogen (N) has a strong defining role on tiller recruitment in tufted grasses that may have evolutionary basis in resource competition.

Some Definitions

A few definitions are necessary. A tiller is an axis of shoot growth with a single apical meristem at its leading end. Tillers are composed of repeated phytomers that are initiated by the apical meristem. A phytomer is a unit which comprises a leaf blade and leaf sheath joined to a sub-adjacent internode at the node, at which is also found a lateral bud. Tillers are initiated by the outgrowth of axillary meristems/ lateral buds at the nodes of parent tillers. So the problem of tillering in grasses is essentially a sub-group of the problem of lateral bud outgrowth in angiosperms. The terms are used interchangeably.

Theories on Lateral Bud Outgrowth/ Tiller Recruitment

Hormonal Control

The hypothesis of direct auxin action (Thimann & Skoog 1933) proposed that auxin or indoleacetic acid (IAA), produced in the apical meristem and young expanding leaves, inhibits lateral bud growth. It seems unlikely that auxin is directly involved with bud outgrowth but may rather be involved with mobilising resources to already differentiating meristems (Sachs & Thimann 1967; Phillips 1975). Subsequently it has been shown that cytokinins are involved in promoting cell division and lateral bud outgrowth (John et al. 1993; Bangerth, Li & Gruber 2000) and cytokinins may be able to mobilise plant nutrients into tissues where they collect (Li, Hagen & Guilfoyle 1992), suggesting that this hormone may be responsible for stimulating bud outgrowth. Lateral branching of apple (*Malus*

domestica) has, however, been stimulated by both a sorbitol and sucrose solution and a cytokinin and sucrose solution (Karhu 1997b), suggesting that bud outgrowth may be stimulated by more than one compound. In addition there is evidence that cytokinin is not the only resource required to stimulate lateral bud outgrowth as some studies have demonstrated higher cytokinin concentrations in buds prior bud growth than after release (e.g. King & Van Staden 1988). Although it is well established that cytokinins are synthesised exclusively in roots, there is strong evidence that shoots are also able to produce cytokinins (Wang & Wareing 1979; Cline 1991).

The most widely accepted hypothesis on hormonally controlled apical dominance is based on the auxin:cytokinin ratio and proposes that auxin produced by the apical meristem and adjacent young leaves blocks the utilisation of root-synthesised cytokinin within lateral buds, thereby inhibiting their growth (Cline 1991). The exact mechanism involved is still not understood, but a mechanism of auto-inhibition of auxin transport from lateral buds has been proposed (Bangerth 1989; Bangerth et al. 2000). In this theory auxin export from dominated lateral buds is inhibited by the dominant meristems. Hence nutrients and cytokinins are directed to the dominant meristems to continue their growth at the expense of the dominated meristems. The authors have demonstrated this auxin auto-inhibition, and note that continued application of cytokinin to the dominated meristems can induce strong growth and ultimately change the order of dominance (Bangerth et al. 2000).

A founding pillar of apical dominance is that removal of the apical meristem often stimulates growth of side shoots (Thimann & Skoog 1934; Leopold 1949). Bangerth et al. (2000) demonstrated that root-derived cytokinin concentration increases dramatically after apical decapitation of pea seedlings. They further demonstrated that this increase could be reduced in a concentration-dependent manner by application of auxin to the decapitated shoot, concluding that auxin may exert control over the production of cytokinins by roots. In turn, cytokinins may increase auxin production by stimulating lateral bud outgrowth, providing a feedback loop.

There is sufficient evidence demonstrating that tiller initiation in grasses is not consistently stimulated following defoliation and/or apical decapitation (review by Murphy & Briske 1992) and may vary among species (Danckwerts & Stuart-Hill 1987). Selective removal of the apical meristem while the leaves remain intact does not consistently stimulate tiller initiation in all grass species (Laidlaw & Berrie 1974; Richards, Mueller & Mott 1988). This suggests that auxin control over lateral bud outgrowth is indirectly inhibitive through control over some other factor, possibly cytokinin. In addition, although

tiller recruitment after defoliation may extend the period of tiller initiation, there appears to be a carryover effect because grazed plants subsequently produce significantly fewer tillers during periods of maximum recruitment on ungrazed neighbours of the same species (Briske & Butler 1988). It is improbable that this effect can be assigned to a restriction on available lateral buds as most lateral buds are below the level of defoliation (Tainton & Booysen 1965a) and these appear to have a long life expectancy (Hendrickson & Briske 1997). This suggests that tiller recruitment must in part be mediated or restricted by some other factor. Hence although evidence for the hormonal mechanism of apical dominance is demonstrable in both dicotyledonous and monocotyledonous plants and therefore is relevant, it is too restrictive an interpretation of tiller recruitment in bunchgrasses (Murphy & Briske 1992).

Resource Availability

The nutrition hypothesis is based on the concept of resource sinks in which apical dominance is maintained by the internal competition among buds for nutrients (Gregory & Veale 1957; Cline 1991). While the nutrient requirements of the existing shoot meristems exceed the supply rate, lateral bud inhibition will be maintained due to nutrient deprivation. Once the nutrient supply rate exceeds the demand rate of existing meristems, the increased nutrient concentration in the shoot stimulates lateral bud outgrowth. Apical decapitation removes the metabolic sink, thereby allowing resources to be redirected to lateral buds, which promotes tillering. Unfortunately comparing the nutrition hypothesis and the auxin inhibition hypothesis directly is difficult because the terminal bud is both a nutrient sink and a source for hormonal production (Cline 1991).

There is definite evidence that resource limitations can restrict tiller recruitment (McIntyre 2001). Tiller initiation on barley grown in a low nitrogen medium was restricted, but could be consistently stimulated at any time by N addition (Aspinall 1961). Decapitated ryegrass plants grown with high N availability produced significantly more secondary tillers than decapitated plants with low N availability (Laidlaw & Berrie 1974). Nutrient additions of N or phosphorus to the soil stimulate bud outgrowth on nutrient-deprived plants (e.g. Daniels 1986; Prasad et al. 1989), and lateral bud growth is also stimulated by directly feeding NH_4NO_3 to cut rhizomes (e.g. McIntyre 1972). Water supply (McIntyre 1968, 1977, 2001; Cottignies & Jennane 1988) and carbohydrate supply (Fletcher & Dale 1974; Blake &

Tchapinski 1986; McIntyre 2001) can restrict bud outgrowth. Six species of tufted grass grown in bags were subjected to different intensities of shading (from no shading through to 30% sunlight) (Everson, Everson & Tainton 1988). Reduced light intensity restricted tiller recruitment on all species, presumably as a result of reduced carbohydrate production. The role of N in overall plant nutrient balance and growth potential is emphasised by the well-established relationship between leaf N concentration and photosynthetic rate (e.g. Cruz 1997). This in turn determines the overall productivity of plants, suggesting that N may play a key role in determining overall plant nutrition status, thereby at least indirectly regulating lateral bud outgrowth. Consequently any recruitment strategy which responds rapidly to changes in plant N status is more likely to utilise periods of high growth potential more efficiently.

Although it is apparent that resource competition has a definite effect on tillering events and tillering rates, there also appears to be strong evidence that nutrients do not act as direct cues for lateral bud activation. Quantitative determinations of endogenous nutrient content before and after bud break have not demonstrated the correlation required by the nutrition hypothesis (Phillips 1975). Mineral levels in inhibited buds can be as high as in uninhibited buds (Phillips 1968) and in peas inhibited lateral buds contain storage starch (Wardlaw & Mortimer 1970). In addition, direct additions of nutrients to inactive lateral buds do not stimulate their outgrowth (Cline 1991). Increasing mineral nutrients apparently reduced lateral branching in honeysuckle (*Lonicera caerulea*) in vitro, while there was a positive linear relationship between the concentration of cytokinin and the number of lateral branches (Karhu 1997a). Additions of N or phosphorous through the root systems of nutrient-deprived plants has a strong promotive effect on bud outgrowth (Daniels 1986; Prasad et al. 1989). This suggests that nutrient additions through the roots stimulate some other growth promoter, which in turn stimulates lateral bud outgrowth. The obvious candidates are cytokinins, N-rich compounds (e.g. zeatin, N^6-dimethylallyladenine, 6-furfuryladenine (kinetin)) that are synthesised in the roots.

The idea that cytokinin concentration was regulated by N was first hypothesised by Kuiper et al. (1988). It has subsequently been proposed that root:shoot partitioning in response to N supply may be mediated by cytokinin and sucrose levels (Van der Werf & Nagel 1996). This idea is given credence by work on *Urtica dioica*, where cytokinin addition to roots induced allocation of exported photosynthate to the apical meristem and away from the roots (Fetene & Beck 1993). Recent studies have shown that there is a positive relationship between N-supply and cytokinin production and secondary tiller

recruitment (Mercier et al. 1997; Takei et al. 2001; Wagner & Beck 1993; Wang & Below 1996). These have indicated that production of cytokinins are stimulated by NO_3^- (Takei et al. 2001), NH_4^+ or mixed N sources (Wang & Below 1996). At the same time overall tillering rates and biomass production were most stimulated by fertilisation with mixed N or just NH_4^+ (Wang & Below 1996). NO_3^--treatment increased the auxin:cytokinin balance, while urea and NH_4^+ shifted this ratio in favour of cytokinins (Mercier et al. 1997).

Photosensitivity to the Red: Far Red Light Ratio

Smith (1982) hypothesised that photomorphogenic responses mediated by phytochrome provide plants with a sensitive mechanism for appropriate adaptation to the changing light environment in plants stands. It was shown that the red light: far-red light ratio (R:FR) changes in accordance to changes in the plant stand density (Holmes & Smith 1975). Secondly, small changes in the R:FR ratio caused large shifts in the phytochrome photoequilibrium (i.e. Pfr/P), allowing phytochrome to be a sensitive detector of plant density (Smith & Holmes 1977). Thirdly, exposure of seedlings to R:FR ratios simulating conditions of vegetation stands revealed an inverse relationship between extension growth and Pfr/P, which demonstrated that signal perception by phytochrome lead to appropriate shade avoidance mechanisms (Morgan & Smith 1978). There is further evidence that perception of changes in R:FR caused by neighbours allows a plant to adapt its strategy before the onset of light competition from neighbours (Ballaré et al. 1987; Ballaré et al. 1997). The predominant effects of the R:FR ratio appears to be organ lengthening and reduced lateral branching (Smith 1982; Casal et al. 1985; Casal et al. 1987a; Skinner & Simmons 1993; Casal et al. 1994). A number of researchers have demonstrated that the R:FR ratio supplied either during or at the end of the photoperiod significantly affects tillering in grasses, where a high R:FR ratio increases tiller production and a low R:FR ratio decreases tiller production (Deregibus, Sanchez & Casal 1983; Casal, Deregibus & Sanchez 1985, 1987a, 1987b; Deregibus et al. 1986; Casal 1988). Shade species are often less responsive to the R:FR ratio than species of open habitats, from which it has been suggested that phytochrome-mediated shade avoidance responses are more advantageous in open habitats than in woodland habitats where elongation elicited by low R:FR beneath the forest canopy would be maladaptive (Morgan & Smith 1979). Within species, sensitivity to R:FR can differ between populations growing in more open versus more shaded environments (Bain & Attridge 1988; Dudley & Schmitt 1995), which suggests that photomorphogenesis

is a selected trait. Hence direct stimulus of lateral buds by R:FR would seem to be an unlikely mechanism for direct control over tiller recruitment which occurs in both shaded and non-shaded environments.

There is a dearth of research on the interaction between R:FR effects and nutrition effects on tillering rates. Only one experiment considered the effect of R:FR on carbon demand (Yanovsky et al. 1995), which demonstrated that FR reduced carbohydrate accumulation in leaves. Research on the effect of N nutrition on the R:FR effect would be most insightful. One experiment (Khattak et al. 1999) has considered the interaction of N supply and light quality (light intensity, R and FR) on plant growth rate in *Chrysanthemum morifolium*. The effect of N on growth was significant and additive, but the effect of light quality was not consistent. High R:FR only increased leaf area on the highest-N treatment, while a reduction in leaf area in response to high R:FR was recorded on the lowest-N treatment although the differences between treatments were small. The R:FR response appeared secondary to plant N-supply in the experiment. Switchgrass seedlings (*Panicum virgatum*) were grown in a factorial experiment of four different planting distances combined with two levels of nitrogen fertilisation and water application (Sanderson & Reed 2000). Tiller recruitment responded positively to planting distance and N application stimulated tillering at all planting densities. However there were no significant differences between N levels or water levels The authors attributed the effect to competition for above-ground resources, but a possible alternative explanation is that tiller recruitment may have been inhibited by plant perception and response to R:FR shifts caused by neighbours (Ballaré et al. 1987) rather than above-ground resource limitation. Importantly, it is clear that stimulation of tiller recruitment by N application can be moderated.

The effect of R:FR on grass tillering rates under field conditions is inconsistent. One season-long experiment conducted in a humid natural grassland to observe the effect of supplemental R on tiller production through the season (Deregibus et al. 1985), indicated a significant increase in tillering rates on R-supplemented grass tufts of one species (*Paspalum dilatatum*) and a non-significant effect on a second species (*Sporobolus indicus*) relative to non-R-supplemented tufts. There was no significant difference in individual tiller mass between R-supplemented and non-supplemented tufts of either species, which again suggests that nutrient supply was non-limiting. Unfortunately no mention is made of soil fertility or soil moisture conditions. A field trial using *Schizachyrium scoparium*, a drought-tolerant caespitose grass, showed that irradiation with R or FR over a twelve-week period did not significantly affect tiller recruitment at the base of established clones (Murphy &

226

Briske 1994). By contrast seedlings on the same species grown under controlled conditions did respond to end-of-day FR supplementation through reduced tiller recruitment and increased leaf elongation (J.S. Murphy & D.D. Briske, unpublished manuscript, cited by Murphy & Briske 1994).

The suggested role for sheaths and axilliary buds as direct signal receivers (Casal et al. 1985, 1987a; Deregibus et al. 1985) is contestable for tufted grasses because they are covered by older sheaths as internodes only expand during the reproductive phase and should not be able to receive radiation signals. Directed FR irradiation of expanding leaves or stems of barley (*Hordeum vulgare*) produces the anticipated results (Skinner & Simmons 1993). Expanding leaves would be suitable sites in terms of anticipatory perception of light competition (Ballaré et al. 1987) because the received signals are instantaneous and independent across time.

The separation between the probable site of photoreception in young expanding leaves and stems (Skinner & Simmons 1993) and the lateral buds responsible for tiller expansion (Skinner & Nelson 1994) suggests that R:FR photoreception by phytochrome provides a signal which stimulates/ depresses some intermediate agent that is directly involved with the control of lateral bud outgrowth. The obvious candidate is auxin, which is synthesised in young, expanding leaves and hence correlates with the likely sight of photoreception. It is plausible that the Pfr/P ratio manipulates the rate of auxin production, with high R reducing auxin production, thereby stimulating or depressing the apical dominance effect (Kraepiel & Miginiac 1997). The evidence for Pfr/P mediation of auxin is mounting, particularly from mutant plant studies (Van Tuinen et al. 1995; Kerckhoffs et al. 1996), which suggest that both phytochromes A and B1 are involved. However contradictory evidence from auxin-overproducing *Arabidopsis* lines demonstrated that regulation of hypocotyl elongation by light and auxin are independent in that species (Romano et al. 1995), so additional elucidation of the underlying mechanisms is required. It has been demonstrated that IAA proteins can be phosphorylated by phytochrome A in vitro, suggesting a molecular mechanism for integrating auxin and light signalling in plant development (Colon-Carmona et al. 2000). The combined evidence suggests that phytochrome sensitivity to R:FR has an indirect effect on tiller recruitment through direct control over auxin production and sink demand of existing shoots. This alters the interaction between auxins and cytokinins and manipulates the distribution of nutrients.

An Integrated Model for Control of Lateral Bud Outgrowth

There is sufficient evidence in the literature that all three mechanisms for lateral bud outgrowth discussed above have real effects. There are few empirical studies that directly compare the relative importance of the mechanisms to rates of lateral bud outgrowth or how this changes according to environmental conditions. However it appears that the three mechanisms discussed all form part of an integrated strategy that that may be true for all angiosperms. Using the accumulated evidence, we propose the following model of lateral bud outgrowth (see Figure 1).

1. *Lateral bud outgrowth is stimulated directly by negative shifts in the auxin:cytokinin ratio.* Lateral bud outgrowth is controlled by the auxin:cytokinin ratio where auxin prevents cytokinin activity in lateral buds both by manipulating cytokinin production in the roots and by directing nutrients towards existing meristems. It is probable that cytokinin directly stimulates lateral bud development while auxin may be involved in involved in ensuring continued growth after the bud has broken from apical dominance. It has been demonstrated that cytokinin application promotes bud outgrowth, and it is well documented that cytokinin stimulates the cell cycle and there is evidence that combined auxin and cytokinin concentrations stimulate cell division (John et al. 1993). Negative shifts in this auxin:cytokinin ratio below some critical value for short time periods ('events') allow some lateral shoots to escape apical domination and begin outgrowth in response to the increased concentration of cytokinins.

2. *Actual bud outgrowth is restricted by nutrient availability.* Tiller recruitment is certainly restricted by carbohydrate limitations, N limitations, water and probably other mineral constituents as well. These are basic building blocks for growth and without them secondary tiller growth cannot occur. However it is unlikely that they act as direct stimulators of growth because their concentrations fluctuate quickly so they do not necessarily reflect environmental cues and trends sufficiently robustly.

3. *The auxin:cytokinin ratio is shifted by stimulatory/depressive controls in the roots and shoots.* By this means the plant may respond more closely to the imposed environmental conditions. Controls in the roots reflect nutrient availability and suitable soil water
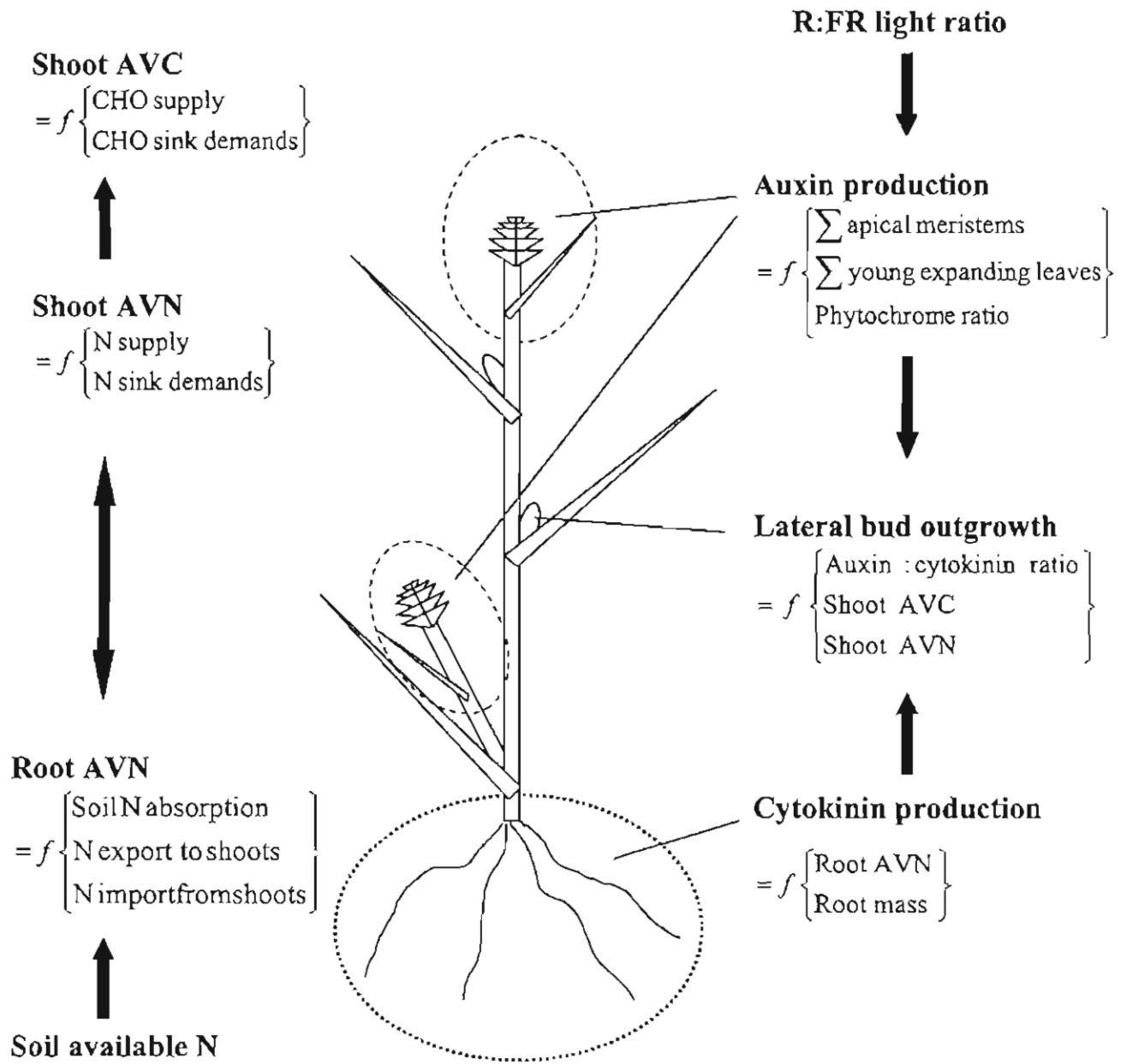
Shoot AVC

$$= f \begin{cases} \text{CHO supply} \\ \text{CHO sink demands} \end{cases}$$

Shoot AVN

$$= f \begin{cases} \text{N supply} \\ \text{N sink demands} \end{cases}$$

Root AVN

$$= f \begin{cases} \text{Soil N absorption} \\ \text{N export to shoots} \\ \text{N import from shoots} \end{cases}$$

Soil available N

R:FR light ratio

Auxin production

$$= f \begin{cases} \sum \text{apical meristems} \\ \sum \text{young expanding leaves} \\ \text{Phytochrome ratio} \end{cases}$$

Lateral bud outgrowth

$$= f \begin{cases} \text{Auxin : cytokinin ratio} \\ \text{Shoot AVC} \\ \text{Shoot AVN} \end{cases}$$

Cytokinin production

$$= f \begin{cases} \text{Root AVN} \\ \text{Root mass} \end{cases}$$

Figure 1 Integrated model of the processes controlling lateral bud outgrowth. All variables are shown as functions (*f*) of the variables that drive them. (R:FR = Red:Far red light ratio; CHO = carbohydrate; N = nitrogen; AVC = available non-structural carbohydrate; AVN = available non-structural N.)

conditions for growth. Controls in the shoots reflect the light environment and photosynthetic potentials.

4. *Auxin export from developing leaves is stimulated/ depressed by the phytochrome equilibrium (Pfr/P), where the Pfr/P is shifted by the R:FR ratio of incident radiation.* Phytochrome has been shown to phosphorylate auxin in vitro (Colon-Carmona et al. 2000), which provides an indirect link between R:FR sensitivity and lateral bud development. The amount of evidence demonstrating this effect is still very small but is increasing.

5. *The phytochrome equilibrium (Pfr/P) manipulates organ size and hence nutrient supply.* By this means the Pfr/P may affect instantaneous growth demands by manipulating organ size in response to R:FR light shifts. Under low R conditions this would direct more nutrients towards lateral buds and away from inactive lateral buds.

6. *Cytokinin production is a function of the concentration of N in the roots.* Cytokinins are high N-compounds predominantly manufactured in roots, so cytokinin production increases sharply during high root N events and is largely depressed during low root N events. High root N events result from increased root absorption of N from the soil as well as sudden mobilisation of stored N when plant growth is reactivated after unfavourable periods such as the winter non-growth season (Bausenwein et al. 2001) or mid-season drought events. Nitrogen concentration in the roots is a function of root soil N absorption rates, rates of export to shoots and within-root conversion to other compounds (e.g. cytokinins), and supply/ sink demands for N storage. The significance is that lateral bud development is probably driven by periods of high root N, which reduces the number of potential bud outgrowth events. Hence lateral bud outgrowth only occurs as short sporadic events within the growing season because N demand by expanding shoots increases with each additional lateral meristem that is stimulated in response to primigenic dominance (Bangerth et al. 2000).

7. *Mediation of lateral bud outgrowth by N is a fixed characteristic across species.* Nitrogen sensitivity is likely to be a fixed characteristic of all angiosperms because N is a highly restricted and seasonal resource across all environments (Seastedt 1995; Blair et al. 1998). It is also a fairly stable signal because changes in soil N availability are not

229

erratic. There is high soil N availability after the non-growing season when microbial activity has been inhibited (Birch 1958) or after burn events which instantly mineralise N from bound shoot sources (Ojima et al. 1994).

8. *R:FR mediation of plant growth is demonstrably flexible species trait.* The ability to adapt R:FR sensitivity/insensitivity is rapid and inherent in at least some species as evidenced by the difference in responsiveness of local populations of the same species. This provides a broad base for evolutionary diversification in different light environments, but the consequences for tillering in nutrient-restricted environments are secondary.

Secondary Tiller Recruitment and the Bunchgrass Functional Growth Form

In this section, tiller growth on bunchgrasses in terms of their growth form and the environment which they inhabit are reviewed in order to assess the evidence for the integrated mechanism of bud outgrowth proposed above.

The Bunchgrass Functional Growth Form

The survival strategy of bunchgrasses contains two components: maintenance of individual genets and propagule dispersion through seedling recruitment. Perennial bunchgrass genets persist through clonal reproduction of tillers and may survive for a substantial amount of time (see Briske & Derner 1998). Optimal clonal growth depends on balancing individual ramet performance and the number of live ramets of the clone in response to the environmental conditions of the site.

Bunchgrasses are composed of closely spaced upright ramets and, importantly, tufts are composed of disconnected clonal units or autonomous ramet groups (Briske & Derner 1998). Consequently intra-tuft competition for available light may be more intense than inter-tuft competition. However live tillers of the same cohort appear to be quite evenly sized across a tuft once they have penetrated the dead canopy layer, which suggests that most clones in the tuft are able to source direct solar radiation. Photosynthetic production is therefore probably not the most limiting nutrient for tillers with some photosynthetic surface

230

exposed to direct light as photosynthesis under direct solar radiation is highly productive. That said bunchgrasses are herbaceous herbs that die back during winter and other non-favourable growth conditions. The rate of decomposition is directly related to moisture availability (Birch 1958; Shackleton, McKenzie & Granger 1989) and the N content of the material (Seastedt 1995), and dead matter can remain in the canopy for a substantial period of time. Hence tillers can be forced to grow through a deeply shaded canopy to reach light, to which etiolated growth is a commonly documented response (e.g. Tainton & Booysen 1965a,b). The response to the R:FR ratio would be significant to cue growth of existing tillers growing through a dense canopy of moribund material where inhibition of secondary tiller production would streamline resource use until the new leaves on existing tillers have penetrated the dead canopy layer. This seems to be contradicted by evidence of tillering on *Themeda triandra* plants at the start of spring under a closed dead canopy when spring regrowth is initiated (Tainton & Booysen 1965a). However there may have been minimal R:FR perception at this time as almost all existing leaf material was dead at the start of regrowth. In addition this may provide evidence for hormonal control as auxin levels would have been low at the start of regrowth, allowing secondary tiller recruitment to occur in response to root N mobilisation and consequent rapid cytokinin production. Primigenic apical dominance would have been established again quite quickly after this initial burst as the tillers grew (Bangerth 1989). Tiller recruitment in spring is a widely documented phenomenon in bunchgrasses (Butler & Briske 1988; Olson & Richards 1988; Murphy & Briske 1994), but the strength of the effect varies among species (Tainton & Booysen 1965a; Tainton & Booysen 1965b). This may relate to differences in instantaneous levels of nutrients arising from the accumulated effects of differences in spring growth allocation to shoots and roots (e.g. Bilbrough & Caldwell 1997) and differences in individual organ growth rates.

Tufted grasslands have the additional characteristic that basal cover is localised under the tufts and there are large interstitial spaces of unoccupied bare ground. Greater tiller recruitment occurs on the edge than on the interior of tufts (e.g. Butler & Briske 1988; Olson & Richards 1988), even after grazing events that make the light environment more uniform across tufts. This indicates that the effect of light quality is overridden by another factor because the homogeneous light environment following fire should have promoted similar tillering rates on both inner and outer primary tillers if R:FR responsiveness were the dominant effect. The difference in tiller recruitment between inner and outer tillers on tufts of caespitose grasses cannot be explained by directed tiller recruitment as this would

imply physiological integration across the tuft, which is invalid for caespitose species (Briske & Derner 1998) though it may have some relevance to rhizomatous species. The most likely explanation is that individual ramet groups on the inside of tufts have smaller nutrient reserves than ramet groups at the edge of tufts. This would be plausible for the considered treatments which all share the property that intertuft canopies are not closed at the end of the growing season. Therefore restrictions on light absorption would be greater for those tillers on the interior than at the edge of tufts, thereby limiting their growth potential and capability for accumulating nutrients during periods when above-ground biomass is large and composed of a large fraction of dead matter.

Soil fertilisation with N and P has a strong positive effect on tillering (Aspinall 1961; Daniels 1986; Prasad et al. 1989). Tufts of *Themeda triandra* and *Kyllinga nervosa* were subjected to a 2^4 factorial design experiment of clipping height, clipping frequency, watering frequency and N level (McNaughton, Wallace & Coughenour 1983; Coughenour, McNaughton & Wallace 1985). Tillering was most strongly correlated to N as were most other morphological traits. Biomass was most strongly correlated with clipping height, while water was only significant to stem biomass, possibly because both water levels were sufficiently abundant. This suggests that tillering rate was not limited by carbohydrate availability even though the regrowth carbohydrate supply of existing tillers subjected to the severest defoliation treatment would have been substantially restricted.

The large interstitial spaces between tufts suggest that competition for sub-surface resources (water and minerals) is a more critical component of inter-tuft competition. Tiller recruitment and growth of the bunchgrass *Themeda triandra* in a humid grassland was concentrated in spring and early summer, declining from mid-summer through to autumn when some recruitment occurred on all treatments (Tainton & Booysen 1965a). There was some tiller recruitment on non-reproductive tillers after midseason mowing, but this could not be attributed to changes in sink demands because the height of the mow would not have decapitated tillers. This suggests that tillers were temporarily released from apical dominance because most or all of the young leaf material responsible for auxin production was removed by the defoliation event. However, subsequent plant growth was limited and tiller recruitment was very low even though incident photosynthetic production potential was high and soil water content was evenly distributed, which suggests that the lack of regrowth was due to soil nutrient limitation. In a similar trial on *Themeda triandra* in a semi-arid region, tillering patterns for non-irrigated versus irrigated tufts (water pressure maintained between wilting point and field capacity) were similar, with substantial

recruitment during spring and little tillering at any other time (Danckwerts, Aucamp & Du Toit 1984), indicating that tiller recruitment was not stimulated by water supply.

Species Effects

There is much evidence to suggest that tillering response across species is a function of non-structural N concentration in the plant. An experiment was conducted in which a pulse of N was supplied to six plant species, either in early, mid or late spring (Bilbrough & Caldwell 1997), where the control treatment involved supplying the same total amount of N in a series of smaller doses every two weeks. The grass species (two annuals and two perennial tussock grasses) recruited tillers more strongly in response to the pulses than to the control, but there was some variation. Of the two perennial species, *Pseudoroegneria spicata* responded equally to each pulse. *Agropyron desertorum* responded much more strongly to the early- and mid-spring pulse treatments than to either the late or control treatments. Leaf N concentration in both tussock species declined progressively through the season on all treatments. N concentration in control plants was always substantially lower than in pulsed plants for each pulse-control pair, but N concentration in the control plants in early spring was higher than the N concentration in late-spring-pulsed plants. Pulsed N supply also increases the N uptake so that N-supply may exceed N-demands, promoting secondary tiller recruitment. Subsequent work (Yoder & Caldwell 2002) suggests that *A. desertorum* is a strong competitor for N, which may explain its much higher tiller recruitment in the previous experiment. It achieves this by early spring root growth and high specific root length relative to *P. spicata* (Caldwell & Richards 1986) which allows *A. desertorum* to capture available soil N more efficiently than the *P. spicata*. Similar apparent competitive advantages have been demonstrated by other species (e.g. Campbell & Grime 1989).

The differential response to N pulses raises intriguing questions: are species differentially sensitive to tissue N concentration with respect to tillering response, or are differences merely the consequence of different growth rates, which in turn determines the total sink demand? It is probable that both are true. Evidence has been provided in the previous section which indicates that some species are sensitive to the type of N supplied, with a positive correlation between lateral bud outgrowth and NH_4^+ absorption and negative correlation with NO_3^- absorption (Wiltshire 1973; Wang & Below 1996; Mercier et al.

1997). This may in part relate to the type of photosynthetic pathway employed, where C_4 species require less N for photosynthetic C reduction than C_3 species (Lawlor 1993).

Ontogenetic plant size and shoot growth rate have both been correlated to the rate of tiller production, providing additional evidence that tiller recruitment is in part determined by sink demand. In the Serengeti, smaller species had lower individual growth rates than the taller species, but the former were able compensate for this by partitioning more resources to many shoots of small size (Coughenour et al. 1985). This suggests that slower shoot growth rates of species with smaller tillers combined with higher root:shoot ratios allow nutrient concentrations to build up to levels where they can recruit secondary tillers on a more frequent basis than species with larger tillers and/or faster growth rates. Light concentrations are less restrictive in short swards and large root: shoot ratios potentially ensure better N growth relative to demands in these environments.

Seasonal distribution of tiller recruitment events appear to be consistent across bunchgrasses although the size of the response depends on species traits. Secondary tiller recruitment in both spring and autumn was a consistently recorded across bunchgrass species growing in a humid grassland whereas recruitment in summer was depressed in the absence of moderate defoliation (Tainton & Booysen 1965a,b; Rethman & Booysen 1968). Defoliation consistently stimulated tiller recruitment, but autumn-flowering species recruited more strongly in response to summer mowing than spring-flowering species. Tiller recruitment was also associated with apical elevation and was a consistent response to apical decapitation during the elevation phase. Some species showed a marked increase in tillering after flowering was complete. The species effect on tillering patterns indicates that tiller recruitment is associated with growth phase. Nutrient demands on flowering culms probably declines once seeds are mature and ready to dehisce, which may allow mobilised nutrients to be re-allocated to secondary tillering during this period (Tainton & Booysen 1965a,b). Whether or not this result is achieved through an associated decline in auxin production is remains to be elucidated explicitly (see Cline 1991).

The evidence suggests that tillering through the season was associated with changes in plant nutrient availability and nutrient mobilisation. Combined with the evidence from the previous section, this suggests that the dominant nutrient involved with tiller recruitment is nitrogen.

The Role of Nitrogen as a Mediator of Tiller Recruitment in Natural Grasslands

The evidence that N is involved with tiller recruitment is incontestable. The question remains as to whether N is directly involved with stimulating lateral buds or merely necessary to supply building blocks for bud outgrowth. The heuristic argument for N as a direct stimulator of tiller recruitment is strong although it has rarely been emphasised in research (Farrar, Pollock & Gallagher 2000). N is generally the most restricted plant mineral nutrient in semi-arid to humid systems (McIntyre 2001). Blair et al. (1998) estimated that between $5.1 - 7.5$ g N m^{-2} yr^{-1} were absorbed by plants of the Tallgrass Prairie, of which $4 - 5$ g N m^{-2} yr^{-1} were absorbed through root absorption, with the remainder made up by bulk precipitation ($1 - 2$ g N m^{-2} yr^{-1}) and N_2-fixation ($0.1 - 0.5$ g N m^{-2} yr^{-1}). Similar estimates are given for the Serengeti system (Coughenour, McNaughton & Wallace 1984). At a density of about 1000 tillers m^{-2} (Coughenour et al. 1984), this converts to $0.0051 - 0.0075$ g N tiller^{-1} yr^{-1}. The estimated accumulated N demand of an individual rooted tiller of the bunchgrass *Themeda triandra* is between $0.0519 - 0.1090$ g N (depending on root:shoot ratio estimates), which is ten times the absorbed fraction. The fraction of N-re-allocation in graminoids is high relative to other growth forms, but at about 0.585 g g^{-1} N (Aerts 1996), this is not sufficient to meet the total demands of individual tillers. As such any strategy which responds quickly to high available soil-N events will grow closer to the integrated optimal growth potential of the grassland environment as set by its most limiting resource. Tiller proliferation is one means by which a clone can take advantage of suitable growth conditions. Clearly a plant that is able to cue tiller recruitment to coincide with suitable resource conditions will have a greater chance of prolonged site occupation. Soil N availability is dependent on rates of N mineralisation resulting from microbial decomposition of dead organic matter. Microbial decomposition responds to soil water content and to intermittent drying that probably kills off a large portion of the soil microbes, thereby releasing N for plant uptake during rewetting cycles (Birch 1958). The largest flush of soil N occurs directly after winter, which coincides with a large recruitment of tillers. Tiller recruitment in autumn (e.g. Tainton & Booysen 1965a,b) may reflect responses to rainfall events after mid-summer dry periods (Birch 1958).

Secondly, availability of soil N is stable and non-erratic, with high relative availability after fire or winter declining to low relative values in the middle and late part of the growing season (Blair et al. 1998) depending on the rates and amounts of structural decomposition (Birch 1958). Absolute values of available soil N are always low in

bunchgrass communities, with maximum values at any one instant being much less than 1% (Blair et al. 1998). Carbohydrate is less likely to provide a direct cue to lateral bud outgrowth because it fluctuates diurnally in response to the photosynthetic cycle (see review by Farrar et al. 2000). However, as carbohydrate is the building block of all plant structures, it must necessarily be involved in determining whether conditions are suitable for tiller recruitment after initial lateral bud stimulation (Karhu 1997b).

Thirdly, soil N absorbed through the roots may stimulate cytokinin production (Wang & Below 1996), depending on the source-sink relationships in the plant. Cytokinin appears to be directly involved with lateral bud activation. Hence grasses growing in a restricted N environment would be able to tiller rapidly in response to increased soil N availability. This initiates rapid shoot growth and concomitant photosynthetic surface that far exceeds the surface that could be supplied by tillers which have not activated axillary meristems. In addition the high N content of the new shoots increases photosynthetic rate thereby further increasing net photosynthetic production. The increased photosynthetic production in turn stimulates further root growth in order to sequester soil N, promoting a positive feedback loop. Running parallel to this, auxin levels would increase rapidly as more tillers are recruited, thereby restoring primigenic dominance (Bangerth 1989). A possible argument against this hypothesis is that once the soil N has been sequestered, shoot sink demands would far exceed N supply placing the plant seriously off-balance. However it appears that young tillers are regularly abandoned (Butler & Briske 1988) so the plant is adapted to withstand this consequence of greater opportunism. In addition N is readily stored as protein in leaf tissues and it is well-documented that leaf tissue N levels decline through the season as the N gets diluted by re-allocation through the plant (Hayes 1985; Heckathorn & DeLucia 1995), allowing grass plants to withstand periods of little or no soil N availability. In addition some N can be re-allocated from leaves to stems, roots and rhizomes in response to drought or winter dieback (Hayes 1985; Heckathorn & DeLucia 1995). Research on tufted grasses indicate that spring regrowth is heavily dependent on remobilisation of old-leaf nitrogen (Bausenwein et al. 2001). We could find no work on N re-allocation after mid-season droughts or whether secondary tiller recruitment is associated with regrowth after drought. Such evidence would further corroborate the role of N as the strongest mediator of lateral bud outgrowth in bunchgrasses.

Acknowledgements

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