BROWSE: QUANTITY AND NUTRITIVE VALUE OF EVERGREEN AND DECIDUOUS TREE SPECIES IN SEMI-ARID SOUTHERN AFRICAN SAVANNAS

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"The tree which moves some to tears of joy is in the eyes of others only a green thing that stands in the way. Some see Nature all ridicule and deformity, and some scarce see Nature at all. But to the eyes of the man of imagination, Nature is Imagination itself."

- William Blake, 1799, *The Letters*

For Benjamin and Isabella

May you grow up to love climbing trees as much as I do...

PREFACE

This thesis is the result of the author's original work except where acknowledged or specifically stated to the contrary in the text. It has not been submitted for any degree or examination at any other university or academic institution.

Signed ………………………….. Date ……./……./……..
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Prof. Kevin Kirkman (supervisor)

ABSTRACT

Browse selection, intake, utilisation, palatability, quality and production are tightly linked and need to be considered together in trying to improve our understanding of browsing dynamics and the interactions between browsers and vegetation. Such an understanding is necessary in order to re-evaluate determinations of browser carrying capacities and evaluating actual and potential impacts of browsing animals on vegetation composition and diversity. Browser carrying capacity is determined by both the quantity and the nutritive value of forage. The measurement of browse quantity and nutritive value and the matching of browse supply to browser demand are central to sustainable utilisation and the monitoring of vegetation health.

South African savannas are poorly studied with respect to tree canopy growth and browse production making it difficult to quantify the available browse biomass on which browsing capacity estimations are based, and consequently difficult to estimate levels of browsing that are sustainable. This study addressed these issues by investigating browse dynamics, broadly aiming to (1) explore factors affecting browse production, biomass and nutritive value; (2) develop models to assess and monitor these parameters across seasons and properties; (3) use the resultant models in improving our understanding of how to determine browser carrying capacities. More specifically, our study sought to examine the effects of plant physiognomy, forage nutritive value, canopy stratum, defoliation, temperature, rainfall and soil nutrient status on the browse production of evergreen (*Carissa bispinosa, Euclea divinorum, Gymnosporia senegalensis*), semi-deciduous (*Spirostachys africana, Ziziphus mucronata*) and deciduous (*Acacia nilotica, Dichrostachys cinerea*) savanna tree species from June 2003 – June 2005 in three sites along the northern Zululand coastline of KwaZulu-Natal.

Available browse biomass, during the dry season, of four key savanna tree species (*A. nilotica, E. divinorum, G. senegalensis, and S. africana*) was estimated through the development of allometric regression equations. Non-linear regression was used to investigate the relation between the leaf dry mass (LDM) and canopy volume (CVol) of each of the four tree species. Exponential regression ($y = a + br^{\ln x}$) of the natural logarithm of CVol data provided the most accurate and precise description of the tree CVol – LDM relation.

A study was undertaken to determine which factors may influence browse production in a southern African savanna. Regression tree models for the browse production identified that the dominant factors influencing browse production were CVol (m^3), season, species and height to the lowest leaves of the tree canopy (HL) (m). The length of the growing season had a marked effect on the production potential of savanna tree species, suggesting that improved conditions for growth, i.e. greater rainfall, soil moisture content and improved soil nutrient availability result in a longer period of rapid sustained growth. Species was identified as an important contributing factor to differences in browse production rates, suggesting the need for the development of species or species group models.

Mean annual browse production of evergreen trees was greater than that of deciduous and semi-deciduous trees. Mean quarterly (three monthly) browse production was highest, for all trees, during the wet season, with the greatest difference between wet and dry season production being observed in deciduous forms. Evergreen forms showed continuous growth over the whole study, with enhanced growth over the wet season. Deciduous forms, on the other hand, concentrated growth in spurts, when environmental conditions became favourable, with most production occurring during a short growing season.

Browse nutritive value was found to be greatest during the wet season, when growth and photosynthesis are at their greatest. Further, browse nutritive value was greatest in deciduous species. Evergreen trees were found to have greater acid detergent fibre (ADF) concentrations than both the deciduous and semi-deciduous trees. By contrast, crude protein (CP) concentrations were greater in semi-deciduous and deciduous species than in evergreen species.

The daily CP requirements for maintenance for an adult impala (45 kg) were met by all species over all three study areas and all seasons. Daily CP requirements for growth and lactation, however, were only ever met by deciduous and semi-deciduous species, though this result was not consistent over study areas and seasons.

Predictive models for the production of browse on deciduous, semi-deciduous and evergreen trees in northern Zululand were developed using multivariate adaptive regression spline functions. The best predictors of growing season browse production in all three tree guilds (defined here as a group of trees having a characteristic mode of living) were primarily measurable tree dimensions, while the prevailing environmental conditions had little impact.

Differences in the production, nutritive value and available browse biomass between the different tree forms and seasons have a profound effect on the determination of browser carrying capacities and need to be incorporated into any game or conservation management plan.

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"In wilderness I sense the miracle of life, and behind it our scientific accomplishments fade to trivia."
Charles Lindbergh

CHAPTER 1. THE PREDICTION AND MEASUREMENT OF BROWSE QUANTITY AND NUTRITIVE VALUE

"A problem well stated is a problem half solved."
C.F. Kettering

Introduction

Given predictions of increased woody plant production in southern Africa as a result of climate change (Bond and Midgely 2000), predictive understanding of woody plant ecology in subtropical regions is critical for the conservation and management of savannas, including both the tree and grass components. The sustainable utilisation of trees and shrubs by browsing herbivores in savanna ecosystems is important both ecologically and economically. Furthermore, the measurement of browsing impacts on vegetation and consequent matching of browse supply and browser demand are essential for the sustainable utilisation of vegetation and the monitoring of vegetation health. These patterns have been poorly studied in the past due to the high variability of browse production (caused by rainfall, soil moisture content, browser impacts, age, competition, leaf senescence to name a few) and browse consumption, reflected in the broad browser diets, and their variability across seasons and years. Consequently, the browse component of savanna ecosystems in southern Africa has received little attention in terms of its contribution to game ranching and wildlife conservation systems. The rapidly expanding game ranching industry in South Africa and the move from single or dual domestic grazing species systems to multispecies grazing and browsing systems have necessitated that we review the importance of browse in wildlife conservation and its role in carrying capacity determinations.

Carrying capacity attempts to describe the productivity of the vegetation in terms of the number of and type of animals that can be maintained in a productive state on an area of land without deterioration of vegetation or soil (Danckwerts and Drewes 1989). Forage intake is a principle factor in the calculation of carrying capacity estimates, because carrying capacity is primarily a function of the browsing and grazing capacity of the veld (Pietersen et al. 1993). Much scientific focus in the past has been aimed at the graze component of savanna ecosystems and consequently, and very little interest or research has been aimed at the browse component. Information regarding the primary productivity of important browse species, the degree of utilisation of the species by different browsers, or the degree of diet separation between browsing animals, is therefore lacking. Calculations of browsing capacity are, as a result, lacking in scientific backing and are generally based on grazing units (GUs) or large stock units (LSUs).

Developing carrying capacity models helps develop understanding of plant/ animal interactions and is not necessarily only used for carrying capacity determination.

Study objectives and approach

This study broadly aims to (1) explore factors affecting browse production, biomass and nutritive value; (2) develop models to assess and monitor these parameters across seasons and properties; (3) use the resultant models in improving our understanding of how to determine browser carrying capacities. With this in mind, this chapter serves to provide a solid literary basis for the study, outlining the two major components relating to the prediction and measurement of browse, namely (1) browse quantity and (2) browse nutritive value, and relating these components to the prediction of browsing capacity and the monitoring of vegetation health. Secondly, it also aims to bring to light the numerous gaps in current scientific knowledge regarding these components. Lastly, a detailed description of the study areas and the thesis content is given.

Background

Browse quantity

A constant debate among game ranch managers and scientists is that of determining the carrying capacity of a given area. “For the individual rancher, the million-dollar question is: how many animals can I keep and how many can I utilise every year?” (Bezuidenhout 2002). This question is mirrored in conservation systems, with uncertainty around issues of overstocking and culling influencing management decision making. The population densities of herbivores are ultimately limited by the availability of their forage resources (Pellew 1983b, Pietersen et al. 1993), while the sustainability of a herbivore population in any conservation or game ranching system is limited by the sustainability of the vegetation. Quantifying forage resources in terms of their temporal and spatial variation is therefore essential, both for understanding the dynamics of herbivore foraging ecology, and for monitoring fluctuations in feed availability and changes in species composition and structure in relation to animal numbers and climatic variation. For grasses, this is relatively straight-forward (t'Mannetjie 2000), but the lack of robust, accurate methods to quantify the available browse resource exists due to the inherent high variability among populations of woody plants. Moreover, many of the existing techniques are often costly in terms of time and manpower.

In attempting to match browse supply to demand, it is important to have a clear understanding of what is precisely meant by browse and available browse. For the purposes of this study,

Browse *is defined as -" the sum total of the plant material produced by a variety of woody species" (Pellew 1981)*
Available browse *is defined as - "the sum total of the plant material produced by a variety of woody species that is potentially edible to ungulates. It comprises all the green leaf and all the young unlignified (i.e. before secondary thickening) shoots of the current season's growth" (Pellew 1983a).*

Browse availability has been determined according to the different feeding heights of browsing ungulates, related to body size and feeding techniques. Additional obstacles in the definition of 'available browse' are that plant parts (particularly leaves, fruits and seed pods) are often eaten after they have fallen to the ground (Owen-Smith 1985) and that animals can actively make forage available by breaking stems or branches, or even pushing the entire tree down (as in the case of elephants) (Owen-Smith 1985). Furthermore, this definition is more difficult to apply in very broken, uneven terrain (Rutherford 1979). Browsers can consume various parts of woody plants, and these may include the leaves, bark, wood, twigs, roots, fruits, flowers and seed pods (Kerr et al. 1970, Owen-Smith 1982). The amount of browse available to ungulate species is therefore a function of the different feeding habits and feeding heights of the different ungulate species as well as a function of the vegetation, in terms of the different growth forms available, the accessibility of the foliage to herbivores, plant-nutrient content (influenced by local climate, soil and geological environment of each plant), and the plant's secondary defences against herbivory. The amount of browse available on each tree species therefore varies from individual to individual and from season to season and thus cannot be considered as a set figure.

For simplicity sake, this study adopts Pellew's (1983a) definition of 'available browse' (above). This definition, however, does not take into account any measure of nutritive value on available browse measures and as a result standing crop biomass may be over-estimated.

Browse biomass

Having identified the available browse in a specific area, there still remains a wide range of possible sampling units (Rutherford 1979). According to Rutherford (1979), some of the basic aspects which make practical sampling difficult are that browse (1) is often not easily distinguishable in a uniform way in the field, (2) it consists of a very large number of small discrete parts, (3) its three-dimensional distribution on the plant is often highly variable and (4) spatial distribution of woody plants can be highly heterogeneous. When considering the ecosystem as a whole, it is important to express browse in the form of mass or energy (Rutherford 1979). At the same time, there is an equally important need to express the mass per unit land area (e.g. kg/ha or g/m^2).

Estimating browse biomass

A number of methods have been proposed for the estimation of browse availability. To quantify browse material, Teague *et al.* (1981) determined total canopy volume and total browse volumes by converting sample data to tree equivalents (TE) and browse units (BU) respectively. A TE was defined as an *Acacia karroo* tree with a height of 1.5 m. These units were designed to quantify available forage (browse) for agricultural systems (Teague et al. 1981).

A common procedure to estimate the mass of browse involves least square regression analysis based on the relation of some easily measurable plant parameter with biomass, determined by destructive sampling (Pellew 1981, MacCracken and van Ballenberghe 1993a). A variety of measurements have been used as the independent variable in regression equations. Rutherford (1979) demonstrates 35 such equations, the simplest of which use regressions based on plant height (Kelly and Walker 1976), stem diameter (Barnes et al. 1976), a combination of plant height and stem diameter (Rutherford 1979) and canopy volume (Kelly and Walker 1976).

Most contemporary models for predicting the carrying capacity of woody browse use the canopy volume of the woody species as the basis for the estimation of available browse (Melville et al. 1999). Canopy volume calculations have proved not only useful in the estimation of browsing capacity, but also in other management areas, such as the ability of the area to sustain fire, habitat selection of certain animal species and the monitoring of bush encroachment and tree growth (Melville et al. 1999).

The most widely recognised browse prediction model in southern Africa is the BECVOL (Biomass Estimates from Canopy VOLume) model developed by Smit (1989a). This method enables the user to calculate the canopy volume of various tree species through the measurement of seven tree dimensions. The estimation of the browsing capacity is then based on those measurements. A relation has been demonstrated between canopy volume and leaf dry mass (Smit 1989b). It can therefore be anticipated that a relation exists between canopy volume and browse availability (Melville et al. 1999).

Browser feeding and selection

The usefulness of available browse biomass estimations for carrying capacity determinations, and for the management of tree species, is somewhat limited by the fact that browsers in Africa seldom actually use more than 10% of the standing plant biomass in any area (Owen and Wiegert 1967, von Holdt 1999) even during the resource limiting periods of the year. In fact some studies have shown utilisation percentages to be as low as 2% of the standing plant biomass (Owen-Smith 1985). Low utilisation patterns of trees may be related to the high selectivity of browsers, in terms of browse species and plant part eaten. Browse utilisation is also influenced by the fact that most of the smaller browsers cannot reach material beyond 2 m (du Toit 1990). Browsing animals tend to focus their consumption efforts on young shoots and new leaves – essentially what has been produced in the current growing season (Smits 1986, Gordon and Illius 1996). Current browser selection research in southern Africa has focused on the selection patterns of black rhino (Ganqa and Scogings 2007), domestic goats (Dziba et al. 2002, Scogings et al. 2004, Dziba et al. 1999), kudu and impala (Owen-Smith and Cooper 1987a, Owen-Smith and Cooper 1988, 1987b). These studies, and others primarily assessed the acceptability of foliage to herbivores and showed it to be influenced by many factors. These factors include (1) nutrients and secondary metabolites (Owen-Smith 1993b, Wrench et al. 1997); (2) physical structures such as thorns (Cooper and Owen-Smith 1986); (3) growth stage of the whole plant and its leaves (Oates et al. 1977); (4) soil nutrient and light availability (Owen-Smith and Cooper 1987a); and (5) previous defoliation history (Rhoades 1985).

Browse production

For the purposes of this study,

***Browse production** is defined as - "the growth or yield of a tree (dry matter) over a given period of time (e.g. 3 months or a year)" (Pellew 1981).*

This definition excludes the increased plant mass attributable to secondary thickening of shoots, as well as the production of wood in stems, branches and roots. In practice, the available browse production is considered as the cumulative increments of new shoots below 5 m (maximum browsing height of a giraffe (Pellew 1981)) over a given period.

In the definition of browse production, a distinction needs to be made between the forage produced as a result of the natural process of growth, and the production of regrowth as a compensatory mechanism in response to defoliation of some kind, whether mechanical or a result of herbivory. Many studies have focused on browse production in the presence of herbivory (Milton 1988, Teague 1989, du Toit et al. 1990, Teague and Walker 1990, Danell et al. 1994, Dekker and Smit 1996, Gadd et al. 2001, Birkett and Stevens-Wood 2005). While herbivory does have a marked effect on the productivity of certain browse species, for example, the *Acacias*, the effect of herbivory varies across different species (O'Connor 1996).

According to Walker (1980), it is important to note that deciduous tree growth is not represented by the initial flush of leaves and twigs in the tree canopy. This flush is a result of the relocation of material stored in the roots and other storage organs during the previous season (Walker 1980). Tree growth actually begins only after the flush, as the current seasonal production of photosynthates increases and more photosynthates are allocated to the growing tips of branches (Walker 1980). While many studies have developed regression equations to estimate biomass and production from various measures, such as plant height, stem diameter and canopy volume (reviewed by Rutherford (1979)), browse production has not yet been accurately measured in southern Africa.

Browse production is closely related to rainfall, tree species and ecological zone (Aucamp et al. 1978, Lamprey et al. 1980, Walker 1980, Pellew 1983a). The available literature from various ecological regions in Africa suggests that browse biomass, especially during the dry season, contributes a large amount of available forage for large herbivores when herbaceous forage is in short supply. In southern Africa, Dayton (1978), in mixed *Combretum apiculatum/C. Zeyheri* bushwillow veld in the Kruger National Park, estimated the standing crop biomass of current shoots considered edible for the two species combined at 1527 kg/ha. In another study in riverine vegetation in north-western Zimbabwe, Goodman (1975) estimated the twig and leaf mass at 2240 kg/ha (Table 1.1). In East Africa, in the Serengeti National Park, Pellew (1981) reported browse productivity rates in the absence of herbivory for a riverine *Acacia xanthophloea* stand reaching 5000 kg/ha/annum (Table 1.1). He also reported a browse production of 1725 kg/ha/annum for *Acacia* ridge-top regeneration thicket (Table 1.1). In Namibia, Rutherford (1978) estimated the annual leaf production of *Burkea africana* woodland savanna to be 1000 kg/ha (Table 1.1). In the semi-arid to humid bioclimatic zones of North Africa, production figures vary from 200 to nearly 1500 kg/ha/annum of edible browse (Le Houerou 1980). While some browse production data is available from north, south, east and west Africa, studies are few and far between, with little standardization to allow direct comparisons. In South Africa, in particular, browse production (as defined by this study) has not yet been measured. Further, very little browse biomass data has been published for KwaZulu-Natal.

Table 1.1: Browse production per annum from a variety of savanna woodland types (taken from: Rutherford 1978, Pellew 1981, Otsyina and McKell 1985).

Plant species woodland type	**Plant part**	**Production kg/ha/annum**	**Study location**	**Author**	**Remarks**
Acacia xanthophloea riverine woodland	New shoots and leaves	5000	Serengeti National Park, Tanzania	(Pellew 1981)	Production of browse below 5.75 m only
Acacia ridge-top regeneration thicket	New shoots and leaves	1725	Serengeti National Park, Tanzania	(Pellew 1981)	Production of browse below 5.75 m only
Colophospermum mopane woodland	Twigs and leaves	1510	SE Zimbabwe, Lowveld	(Kelly 1973)	Range 590 – 2120 sample size = 9
Riverine *A. Xanthophloea*	New twigs and leaves	6000	Serengeti National Park, Tanzania	(Lamprey et al. 1980)	High proportion of mature wood; not for browse
Dry miombo woodland	New twigs and leaves	2528	West-central Zimbabwe	(Martin 1974)	90% of total biomass was wood
Open alluvial woodland	Twigs and leaves	2254	Lutope River, Zimbabwe	(Goodman 1975)	50% higher than 5m, 38% below 2.5m
Colophospermum mopane woodland	Twigs and leaves	1451	SE Zimbabwe	(Kelly and Walker 1976)	Shrubs contribute 12% to total woody biomass
Acacia tortilis ridge-top thicket	New shoots and leaves	1500	Serengeti National Park, Tanzania	(Lamprey et al. 1980)	48.9% of canopy volume of regenerated woodland
Mixed tree and shrub *Burkea africana* woodland	Leaves and twigs	1336	SW Africa Savanna	(Rutherford 1979, Rutherford 1978)	Shrubs contribute 12% to total woody biomass

Determinants of tree growth

The growth of a tree is determined by the tree's genetic potential and the environment in which it grows. The availability of light, water and nutrients are key environmental factors influencing plant growth. Other environmental determinants of vegetative growth of trees include soil water availability and water stress (Tinley 1982, Milton 1988), soil nutrient availability (Bell 1982, East 1984), carbohydrate reserves and plant hormones (Teague 1983, 1988b, Teague and Walker 1988a), tree age (Milton 1987, Novellie 1989), competition (Smith and Goodman 1986), defoliation and shoot pruning (Milton 1988, Stuart-Hill and Tainton 1988, du Toit et al. 1990) and various soil and climatic conditions (Patten and Ellis 1995).

In the estimation of woody biomass and production, regression equations have been developed from various plant physical dimensions, such as stem diameter, plant height and canopy volume. While many of the resulting equations are similar in form, it is evident that each tree species needs to be considered separately (Walker 1980).

1) Light

Trees in savannas and more arid environments, where water is limited, tend to be widely scattered in their distribution. Light interception and the competition for light between neighbours is often not a limiting factor for growth (Scholes and Walker 1993).

2) Temperature and daylength

In temperate regions, temperature and daylength (photoperiod) changes in late winter/spring control the onset of leaf flush and growth (Archibald and Scholes 2007). Temperature reduces tree productivity by limiting the extent of the growing season (defined as the frost-free period in temperate regions), affecting the rate and timing of growth and modifying the rate of photosynthesis (Teskey et al. 1987). Savanna leaf initiation at the start of the growing season appears to be related more to changes in temperature than to rainfall (Rutherford and Panagos 1982, Milton 1987), although daylength has also been identified as a possible factor (Milton 1987). Since savanna trees commonly initiate leaf flush prior to the start of the rainy season (Milton 1987, Zietsman et al. 1989) it is plausible that rainfall is not the proximate trigger.

3) Water

Soil water availability, water stress (Tinley 1982, Milton 1988) and rainfall (Tinley 1982, Shackleton 1999) have been shown to be some of the limitants of vegetative growth in trees. Within arid regions, Le Houerou (1980), reported a general positive relation between total annual rainfall and total woody plant production. In a study of the effect of low rainfall and the browsing of elephant and giraffe on enclosed savanna habitats in Laikipia, Kenya, Birkett and Stevens-Wood (2005) concluded that tree growth does increase rapidly at high rainfall but, at low rainfall, growth does not respond to rainfall and remains at a very low rate. Shackleton (1999) hypothesized that community phenology and productivity would vary along moisture gradients. In his study in the central lowveld, rainfall zone appeared to influence (1) the onset and magnitude of leaf emergence, (2) the lifespan of mature leaves, and (3) the proportion of leafless trees. The onset of tree growth initiated in savanna trees in response to temperature changes at the beginning of spring, appears to be governed by the residual soil moisture, where leaf emergence occurs only when the residual soil moisture is sufficient (Dekker and Smit 1996, Scholes and Walker 1993). According to Scholes and Walker (1993), once tree growth has been initiated, the rate of growth is controlled by nutrient supply rate. Further, the length of the growing period is controlled by soil water availability (Scholes and Walker 1993).

4) Growing season

Although the production of woody foliage is more predictable over time than that of grasses (Owen-Smith 1982), most savanna trees do exhibit a distinct growing season, producing new leaves before the first rains. Hofmann (Shackleton 1999, 1989, cited by), investigated community phenology in subtropical thicket and karroid shrublands along a rainfall gradient in the south-eastern Cape, and concluded that increasing aridity resulted in a concentration of phenological activity into a shorter period. Scholes and Walker (1993) suggested that growing season length is influenced by the carry-over of soil moisture, which is likely to be lower at more arid sites. Shackleton (1999) recorded a greater productivity of sites in greater rainfall areas, but suggested that this productivity may be related to a longer growing season, rather than the greater rainfall per se, although the two are generally correlated.

5) *Soil fertility*

It is generally accepted that browse production increases with increasing soil fertility (Adcock 2001, Prins and van de Jeugd 1992). In semi-arid savannas, tree productivity is constrained by the uptake of nitrogen (N) and phosphorus (P) (Adcock 2001). A plant's production rate is constrained by its N metabolism, while the availability of soil P can influence the rate at which microbial decomposers mineralise nitrogen (Adcock 2001). The size of the mineral pool in the soil and the soil water availability control the rates of mineralization, and the resultant nutrient uptake by the trees (Adcock 2001, Bell 1982).

6) *Tree guild*

Most African savanna trees are thought to be deciduous (Scholes 1997). Further, in general, it is thought that as the annual rainfall decreases and as the seasonality of rainfall increases, the proportion of drought-deciduous species increases (Frankie et al. 1974, Choat et al. 2005). The tree component of African savannas, however, are actually made up of a mix of evergreen and deciduous (of varying degrees) species (Eamus and Prior 2001). The co-occurrence of evergreen and deciduous species in African savannas, suggests that being deciduous is not an essential seasonal drought survival trait. Rather, it seems, deciduous and evergreen species employ different strategies to deal with the same conditions (Choat et al. 2005). In general, African deciduous trees respond to periods of low moisture availability and high evaporative demand by shedding their leaves. Their evergreen counterparts must, under the same conditions, prevent desiccation by maintaining water transport to their canopies at a sufficient rate (Holbrook et al. 1995 cited by, Choat et al. 2005). The resulting differences in the annual pattern of canopy fullness and growth between the two guilds (defined here as a group of trees having a characteristic mode of living) have a profound effect on the rate, quantity and seasonality of browse production and therefore the management of browse resources for browsing ungulates.

Evergreen species retain a full canopy all year round and the decline in canopy fullness in the dry season is less than 10% (Williams 1997). Deciduous species, in contrast, lose all leaves for at least one but usually two to four months of each year (Williams 1997). A third possible guild is 'semi-deciduous,' i.e. the incomplete loss of leaves during the late dry season, with the extent of deciduousness varying with years, sites and individuals (Eamus 1999, Do et al. 2005). The evergreen or deciduous nature of a tree largely affects the rate, seasonality, and degree of plant growth and production, due to its affect on the plant's net rate of energy capture (Givnish 2002). In general, evergreen trees have the following ecological advantages over deciduous trees: (1) Photosynthesis is potentially conducted over a longer period of each year, even into the dry season (Mooney and Dunn 1970). (2) Evergreen trees have a lower annual cost of constructing the carbohydrate skeletons of leaves, provided that their leaves are retained for more than a year (Givnish 2002). For example, if an evergreen holds its leaves for three years, then it must replace only a third of its canopy each year. (3) Evergreen trees also have a lower nutrient replacement cost (Givnish 2002). Before leaves are shed (whether evergreen or deciduous), the mineral nutrients (e.g. N, P, K) are incompletely withdrawn, and the fraction not re-translocated must be replaced when new leaves are produced (Chabot and Hicks 1982). The more frequently that leaves are shed, the higher the replacement energy costs. This suggests that evergreen trees growing on nutrient-poor soils have an ecological advantage (Givnish 2002). (4) Finally, evergreen leaves often are tougher and thicker than deciduous leaves in order to withstand drought during the dry season without wilting (Chabot and Hicks 1982). Since evergreen leaves are often the only leaves exposed to browsing herbivores during the dry season, evergreen trees invest in tough leaves and high levels of chemical defences to deter (to some extent) high levels of browsing (Coley et al. 1985).

The potential advantages of deciduous trees are: (1) A higher relative photosynthetic capacity as a result of their higher leaf nitrogen content. Deciduous trees maintain higher rates of photosynthesis per unit leaf mass during favourable growing conditions than evergreens (Givnish 2002). (2) Since deciduous leaves are adapted only to moister conditions during the wet season, they have thinner cross-sections, higher stomatal conductance and hence, higher mesophyll photosynthetic capacity per unit leaf mass (Givnish 2002). (3) Finally, transpiration is greatly reduced in deciduous trees during the dry season, as without leaves, no leaf respiration can occur (Givnish 2002).

7) Tree age and size

The final shape and size of a tree is a trade-off of all the conflicting requirements of the various plant functions, from growth and reproduction to defence (Archibald and Bond 2003). The size and shape of an adult tree is then not only a reflection of the present conditions under which it is growing, but is the result of all the genetic and environmental factors that have shaped it as it grew from seedling to maturity (Archibald and Bond 2003). The current size and shape of a tree (its height, canopy size, trunk width and rooting area and depth), while a function of previous growth, is also then a determinant of current and future growth.

Browse nutritive value

Nutritive value

The concepts of browse, available browse, browse utilisation and browse production were discussed at length above. What is noteworthy here is that browse being available does not necessarily mean that it will be eaten because of forage preferences. Browsers select among plant species as markedly as grazers do (Grunow 1980).

A preferred forage species is defined as "one which is proportionally more frequent in the diet of an animal than it is in the available environment"; and forage preference as "the extent to which forage is consumed in relation to its availability"' (Petrides 1975).

A principal forage species is described as one making a large contribution to the diet (Grunow 1980). Owen-Smith and Cooper (1987a) distinguish between two basic categories of acceptability of woody species to browsing animals: (1) species favoured year round; and (2) species generally rejected, except during certain periods. Walker (1980) concludes that the degree of utilization of woody species is dependent on the tree species that are present, their relative palatability, their growth form as well as the structure of the herbivore community that is present. In addition, woody plant chemical defences appear to have a large influence on the actual intake of available browse (Bryant et al. 1992). The nutritional characteristics of leaves in different phenological stages may further affect browse acceptability (Hall-Martin and Basson 1975, Cooper 1982, Owen-Smith and Cooper 1987a, Cooper et al. 1988).

While it is difficult to determine what is considered palatable to different browsing species, characteristics that seem to improve palatability are crude protein content, a high concentration of minerals and a high moisture content (Taylor 1969, Walker 1980, Bergström 1992). A high fibre concentration, together with the presence of high levels of chemical defences such as tannins and aromatic substances, reduces palatability (Bergström 1992, Walker 1980, Harbourne 1991). The growth form of a tree, as well as the density of a stand of trees can also influence its perceived palatability by limiting the access to browse material, either through height or a physical barrier (Walker 1980). Barnes (1976) concluded that a proper understanding of animal-plant relations in terms of intake would depend on knowledge of the diet of the animals, the amount of different species on offer and their distribution and availability.

In general, deciduous tree species are thought to be more palatable than evergreen tree species, because evergreen leaves have more inherent physical and chemical defences to reduce browsing (Eamus 1999). Deciduous leaves contain more nitrogen (per unit dry weight), allowing them to photosynthesise more efficiently (Medina and Francisco 1994, Reich et al. 1992) and usually have a larger specific leaf area (leaf area divided by leaf dry weight) than evergreen leaves (Sobrado 1991, Eamus and Princhard 1998, Eamus 1999). This extra N makes them more attractive to browsers. The higher concentration of N in the leaves also increases the efficiency of photosynthesis, allowing the plant to compensate for their short lifespan (Eamus 1999).

Browse nutritive value determinants

Bell (1982) proposed that food nutritive value is indicated by the ratio of easily digestible plant metabolic (M) constituents (cell cytoplasm containing proteins, several minerals and soluble carbohydrates) to difficult to digest structural carbohydrate constituents (C) `(cell walls: cellulose, hemicelluloses, lignin, and cell wall bound secondary chemicals). He further proposed that this M:C ratio is influenced by soil nutrient availability. Plant palatability is largely affected by the balance between the extent of carbon and nitrogen assimilation (Bell 1982). More N assimilation leads to the formation of more plant metabolic constituents (M), and possibly N based secondary chemicals, while more carbon assimilation leads to the formation of more plant structural material and carbon-based secondary chemicals (C) (Bell 1982).

1) *Soil fertility*

It has been observed that the biomass of large herbivores is greater on fertile than on infertile soiled areas, even when the standing biomass of vegetation and rainfall is similar (Bell 1982, East 1984). Little work in southern Africa has focused on the direct effect of soil fertility on browse nutritive value, although the nutritive value of browse has been related to soil fertility in oak-hickory forest habitats of western Tennessee (Fuller and Amundsen 1987). Food nutritive value is therefore a key constraint on herbivore carrying capacity for any area.

2) *Temperature*

Together with rainfall and soil moisture, temperature also affects plant palatability. Ellery *et al.* (1995) proposed that carbon and nitrogen assimilation in plants occur at different temperatures, carbon assimilation at a lower temperature optimum of 25-28^{o}C and nitrogen assimilation at 35-40^{o}C. They further proposed that N assimilation continues in soils too dry to permit plant stomatal opening. Carbon assimilation continues in soils that are nearly saturated, where nitrogen has often been leached out of the system. As a result, cool, wet conditions favour carbon assimilation, while, hot, dry conditions favour N assimilation (Ellery et al. 1995).

3) *Tree guild*

Eamus (1999), proposes the increase in leaf construction costs with increasing leaf longevity. The longer the lifespan of a leaf, the higher the probability of herbivore damage to the leaf, resulting in long-lived leaves containing more defensive compounds and/or structures (Eamus 1999). Deciduous trees, having shorter-lived leaves, need to have high photosynthetic rates, requiring a large investment of N (Eamus 1999, Givnish 2002, Singh and Kushwaha 2005). Evergreen trees, with long-lived leaves, reduce the probability of herbivore, insect and drought damage by having a larger M:C ratio, with a low N content and greater structural carbohydrate constituents (cellulose, hemicelluloses and lignin) (Eamus 1999, Bell 1982).

4) Tree age

The nutritional nutritive value of browse for browsing herbivores reduces with leaf and shoot age (Bell 1982). This is due to the tendency of plant protein production to be reduced at an earlier phase of growth than structural production (Milthorpe and Davidson 1966, Bell 1982).

5) Plant defences

Many savanna woody plants possess physical or chemical defences against herbivory (Owen-Smith 1982, Owen-Smith 1993b), usually interpreted in terms of the resource availability or carbon-nutrient balance hypotheses (Coley et al. 1985). Species growing on nutrient-rich substrates tend to rely on physical defence and rapid growth, characterised by *Acacia* species, whereas species on nutrient-poor substrates, usually unarmed broad-leafed species, invest mostly in carbon-based chemical defences (O'Connor 1996).

5.1) Chemical defences

Chemical compounds have either a potentially toxic or a digestibility-reducing effect on herbivores (Owen-Smith 1982). Toxic compounds include various alkaloids and seem to be more common in herbaceous plants. Compounds that reduce digestibility are more typical of woody species and include tannins and fibre fractions (Bergström 1992).

Chemical mediation of interactions between woody plants and herbivores has been the focus of much research (Bryant et al. 1991). Studies conducted at Nylsvlei in the Northern Province, as part of the Savanna Biome Project, demonstrated links between soil nutrient status, plant palatability, and physical versus chemical defences of plants against large mammalian herbivores (Bryant et al. 1989, Cooper and Owen-Smith 1986, Owen-Smith and Cooper 1987a). Chemical defences are known to deter defoliation by herbivores by being poisonous, bitter tasting or by having anti-nutritional effects (Harbourne 1991). Plant chemical defences can be divided into two broad categories, quantitative and qualitative (Feeny 1976). Quantitative defences reduce digestibility and are effective only with large defensive investment by the plant (e.g. tannins) (Rooke 2003). Qualitative defences, on the other hand, are effectively toxic in small concentrations (e.g. glucosinolates) (Rooke 2003). Further, based on biosynthetic origin, secondary metabolites are divided into three main classes of compounds, terpenes, phenolics and nitrogen-containing compounds (Harbourne 1991).

Terpenes are recognized as phytoalexins, insect antifeedants, pheromones, defence agents, allelochemicals, or signal molecules (Harbourne 1991). Some terpenes are highly toxic to animals while others have the ability to interfere hormonally with animal growth and reproduction (Harbourne 1991).

Phenolic metabolites have been shown to affect food selection, intake and digestion of mammalian herbivores (Harbourne 1991). Plant polyphenols that have received the most attention as potential herbivore defences are tannins (Harbourne 1991). Condensed tannins (CT) are defined as polyphenols which have the ability to bind with protein' (Harbourne 1991). While some browsing herbivores can produce salivary CT-binding proteins (Robbins et al. 1987a), tannins can still reduce protein availability to browsers (Robbins et al. 1987b). In support, some studies have shown a negative correlation between herbivore selection and the concentration of CT in different tree species (Cooper and Owen-Smith 1985, Cooper et al. 1988, Pellew 1984b, Owen-Smith 1993b)

Patterns in phenolic chemistry are evident among woody plant families commonly represented in southern African savannas. Highest leaf concentrations of CT have been recorded among species in the Caesalpiniaceae (*Schotia brachypetala, Burkea africana*), Anacardiaceae (*Ozoroa paniculosa, Sclerocarya birrea*), and Ebenaceae (*Euclea* spp.), especially among evergreens (Owen-Smith 1993b). With the exception of *A. nilotica* and *A. karroo*, members of the Mimosaceae and Papillionaceae generally show low levels of phenolics (Owen-Smith 1993b). Species in the Combretaceae are commonly high in total phenolics, but low in CT, suggesting a predominance of hydrolysable tannins (Owen-Smith 1993b).

Nitrogen-containing metabolites, of which alkaloids are the most well known, have a more restricted distribution in plants compared to phenolics largely due to the limited supply of N to plants (Harbourne 1991). Despite these metabolites usually being produced in low quantities, they are mobile within a plant and are highly toxic to mammals (Harbourne 1991).

5.2) Physical defences

Woody plants with highly nutritious foliage, such as African *Acacias,* are characterised by thorns and spines (Owen-Smith 1982). The thorniness within a species has been shown to be affected by: (1) the age of the plant (Cooper and Owen-Smith 1986) and (2) browsing (Young and Okello 1998). The thorniness of species has been shown to decrease as they grow to tree heights out of reach of browsers (Owen-Smith 1982). Thorns modify the relative acceptability of the plant species possessing them to mammalian herbivores, by restricting the bite sizes that the browsing ungulates obtain, thereby increasing the handling time per unit of forage ingested. Therefore, despite the high nutritional value of their leaves, spinescent species are favoured no more highly than unarmed species (Cooper and Owen-Smith 1986). This effect is influenced by leaf size: the larger the leaf size the less the effects of the thorns and this is modified by the body size and feeding technique of particular animal consumers (Cooper and Owen-Smith 1986).

Management considerations: concepts of carrying capacity

Carrying capacity cannot be considered to be a fixed, static property of the habitat in question, but rather it changes from year to year, depending on, for example, rainfall quantity and distribution, fire regime, extent of herbivory, and condition of the vegetation. Carrying capacity estimates are also influenced by the land-use objectives of a particular property. In a system geared toward the provision of trophy-quality animals, for example, overall numbers should be kept low (Grossman et al. 1999). Where the objective is the production of scarce or endangered animals, stocking rates of competitive species should be low or zero (Grossman et al. 1999). Decisions on the number of animals to stock therefore depend as much on the management objectives as on the primary productivity of the vegetation (Grossman et al. 1999).

Early ecological studies of large African herbivores implied that large herbivore communities could be stocked safely on natural veld at higher rates than domestic herbivores (Talbot et al. 1965 cited by, Mentis and Duke 1976). Not surprisingly, however, in view of the complex plant-herbivore relations in African big-game ecosystems, little material progress has been made in estimating carrying capacities for game. Among others, Jarman (1974) has corrected earlier notions that African large herbivores are ecologically isolated because different species eat different plants, recording considerable overlap in plant species eaten among different herbivores, although their selection for parts of plants varied.

Determining browsing capacities

Few reliable guidelines exist for calculating carrying capacities for large mammalian herbivores that prefer browse rather than graze. This may largely be due to the fact that many such herbivores are small, non-gregarious, secretive and difficult to census. Lamprey (1964) and Mentis (1970) record that such browsing animals make a small contribution to the total stocking rate. According to Mentis (1977), even if population densities of these animals have been under-estimated, the general conclusion is hardly likely to be affected because many of these ‘browsers’ are small and extremely high densities would be required to affect the total stocking rate appreciably. On the other hand, the category of browsers may include eland and nyala (Mentis and Duke 1976), which eat considerable quantities of grass, probably bringing these animals into competition with the bulk grazers, thereby making the accurate determination of their respective carrying capacities imperative to game ranch management.

When attempting to set wildlife stocking densities for conservation or ranching systems, especially for a diversity of grazers and browsers of different sizes, traditional methods of determining carrying capacities are vague and somewhat unsatisfactory. The setting of stocking densities for wild herbivores requires quantitative data on the capacity of the plant resources to support herbivores (Bothma et al. 2004). Models have been described whereby the available quantity and to a lesser extent, nutritive value of browse (Barnes 1976, Rutherford 1979, Teague et al. 1981, Smit 1996) of each plant community on a given ranch or nature reserve can be calculated by using information from appropriate plant ecological surveys. For determining the grazing capacity of a system, grass biomass and species palatability are sufficient because grazers are generally less selective in their foraging, in terms of plant parts, plant species, and to a certain extent (in the case of bulk feeders) plant age. Browsing herbivores on the other hand are highly selective feeders, utilising a small percentage of the available browse biomass (up to 10%) (Owen and Wiegert 1967, von Holdt 1999), selecting for new shoots, and young plant material. Determinations of browser carrying capacity, based on available browse biomass estimates are therefore greatly inflated. It was for this reason that our study was initiated; with the aim of modelling browse production rates of different key savanna tree species, in the northern Zululand region of KwaZulu-Natal, with the assumption that browse production equates to utilisable browse biomass.

Study areas

Location

This study was undertaken in the open wooded grassland areas of three game reserves in north eastern KwaZulu-Natal, Bonamanzi Game Park (BGP), Mun-Ya-Wana Private Game Reserve (MGR), and Pongola Game Reserve (North) (PGR). All three properties are situated in the Maputaland region of northern KwaZulu-Natal, South Africa. The region forms part of the almost flat low level coastal plain which runs from the Umfolozi River, north into Mozambique (Maud 1980). Maputaland is bounded by the Indian Ocean to the east and the Lebombo Mountains to the west. The three study areas are situated on an approximately north/ south axis along the northern Zululand coastline and are situated along a distinct rainfall and temperature gradient (Figure 1.1).

Bonamanzi Game Ranch is situated on the east coast of northern KwaZulu-Natal between approximately 28° 01’ S and 28° 05’ S; 32° 16’ E and 32° 21’ E. The eastern boundary borders False Bay, of the Greater St. Lucia Wetland Park. The property comprises 3950 ha, with a total fence perimeter of 23.7 km. The village of Hluhluwe is situated 3 km northwest of the north-western corner of the ranch and the Hluhluwe-Umfolozi complex is situated approximately 25 km northwest of the ranch.

Mun-Ya-Wana Private Game Reserve (27^{o} 40’ S to 27^{o} 55’ S; 31^{o} 12’ E to 32^{o} 26’ E) is approximately 30 km from the eastern coast of KwaZulu-Natal and covers an area of 23 453 ha. Over 95% of the reserve lies beneath 100 m above sea level (asl) with a minimum altitude of 4 m asl and a maximum of 201 m asl where the southern tip of the Ubombo mountains run through the reserve in its south-west. Mun-Ya-Wana Private Game Reserve has two rivers, the Mzinene which forms the boundary in the south and the Mun-Ya-Wana which bisects the reserve.

Pongola Game Reserve was the northern most study area, located near Golela, the northern border post between KwaZulu-Natal and Swaziland, some 34 km from the town of Pongola (27° 21’ to 27° 33’ S and 31° 52’, 32° 1’ E). It is approximately 6816 ha and surrounds part of the Jozini dam.

Vegetation

According to Camp (1997), the vegetation can be described as Lowveld (Bioresource Group 22). The Lowveld lies below 450 m and has a total area of 879 830 ha, second only to the Moist Coast Forest, Thorn and Palm Veld in size (Camp 1997). It lies mainly north of the White Mfolozi River, with only small areas to the south of the river, and extends to the northern border of KwaZulu-Natal with Swaziland and Mozambique (Camp 1997). The topography is mainly flat to undulating, with the occasional hill (Camp 1997). The exception is the slopes of the Ubombo Mountains, and the Lowveld extends up both the eastern and western slopes of the range (Camp 1997).

Acocks (1988) broadly defined the dominant vegetation structure as savanna and the vegetation pattern varies from open woodland to bushland thickets. These thickets can include, and are often dominated by, species such as *Dichrostachys cinerea, Gymnosporia senegalensis, Acacia nilotica, A. karroo, A. senegal, Spirostachys africana, Euclea crispa* and *Euclea divinorum* (Camp 1997).

Other commonly occurring trees are *A. gerardii, G. heterophylla, Ziziphus mucronata, Combretum molle, Olea europaea* subsp. *africana, Ozoroa engleri, O. paniculosa* and *Strychnos* spp. (Camp 1997).

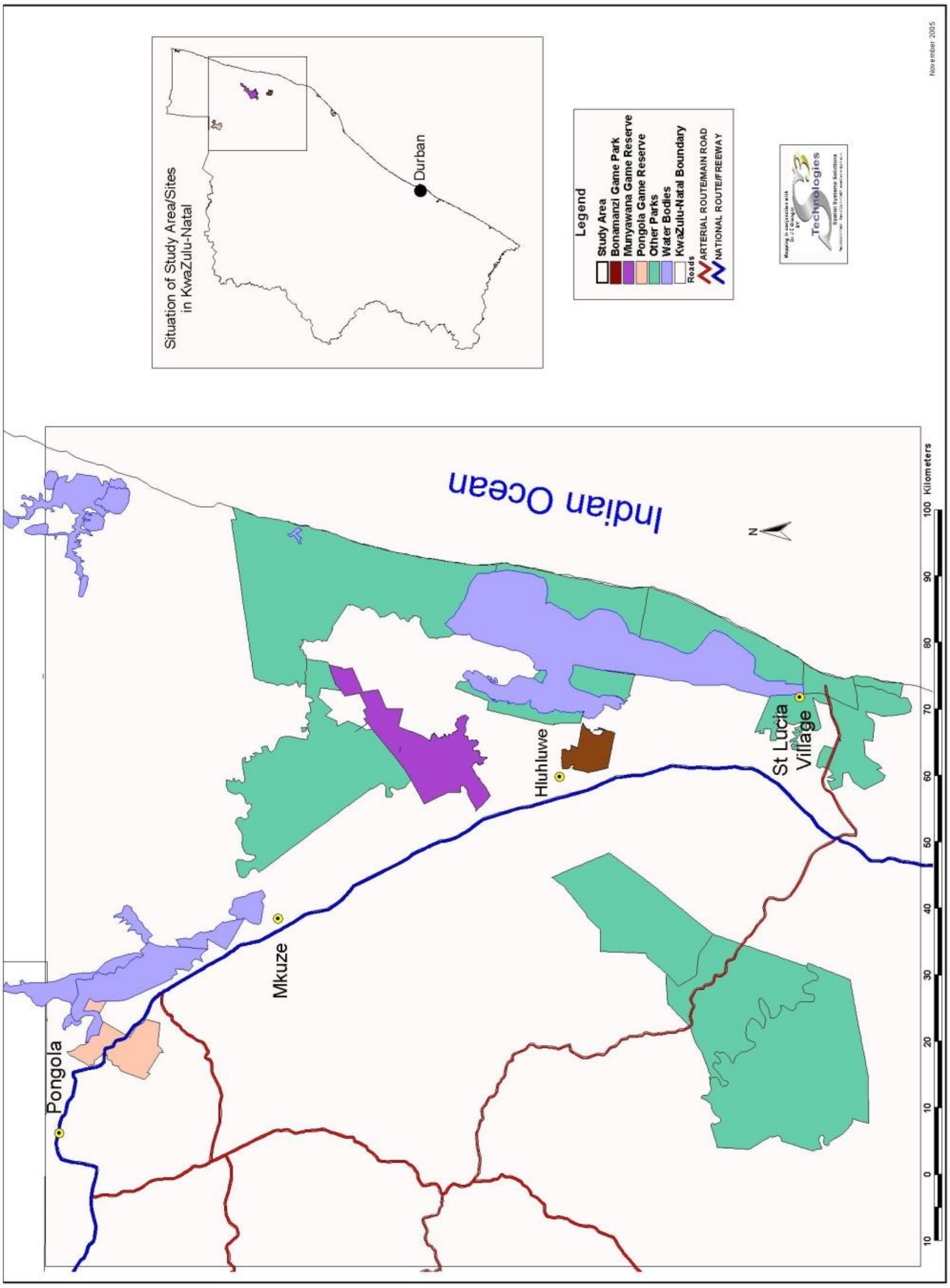

Figure 1.1 : Location of study areas along the northern Zululand coastline of KwaZulu-Natal.

Climate

Maputaland can be described as having a warm to hot, humid sub-tropical to tropical climate (Matthews 2005). Average monthly humidity is relatively high (fluctuating between 65-85%), even in the drier inland parts of the region. The most striking feature of the climate of the Maputaland is the variation in rainfall across the region. The climate is moister along the coast where rainfall is over 1000 mm per annum. Further inland, the mean annual rainfall drops to less than 600 mm (Maud 1980). These annual rainfall values, however, can vary dramatically between years. The area is subject to extreme rainfall events caused by tropical cyclones or cut-off low pressure systems (Matthews 2005). Winters are drier than summers and there is a pronounced dry season (April to September), although rain is received throughout the year, January being the wettest month and July the driest (Camp 1997) (Figure 1.2). Fire is a typical phenomenon during the dry season at intervals varying from one to fifty years (Huntley 1982, 1984).

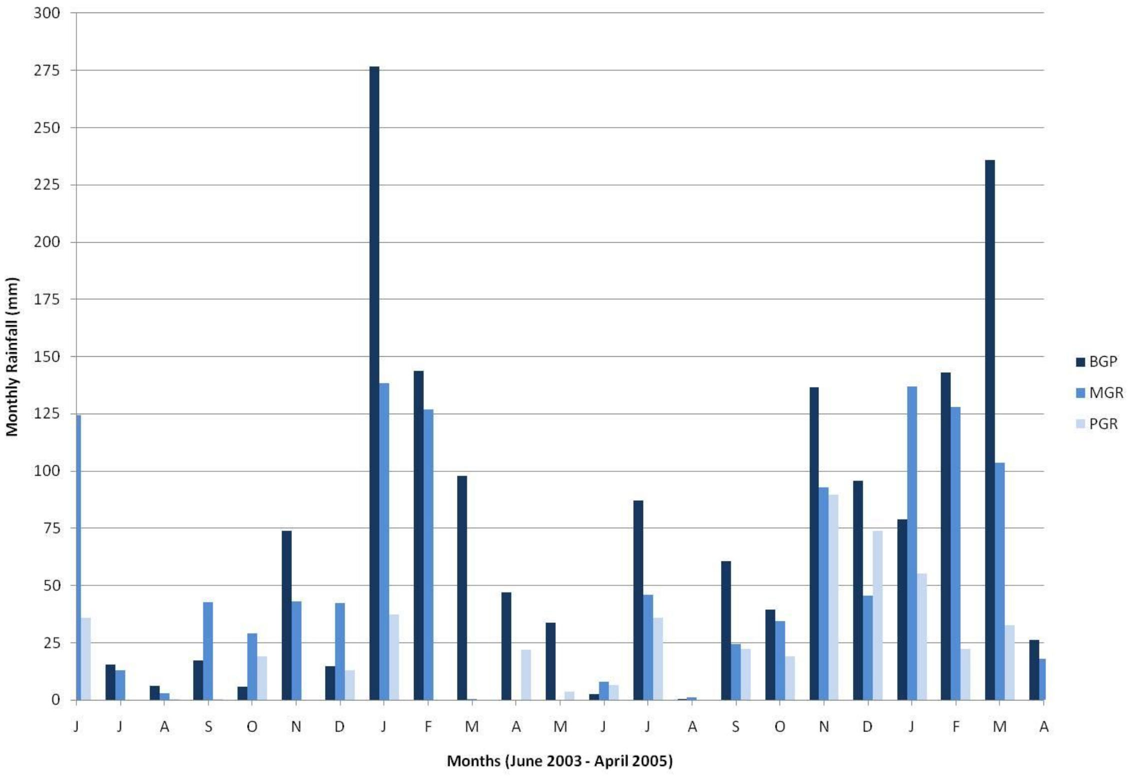

Figure 1.2: Monthly rainfall for the study period, June 2003 to April 2005. Data from Charters Creek weather station for Bonamanzi Game Reserve (BGP), from Mkuze Game Reserve weather station for Mun-Ya-Wana Private Game Reserve (MGR) and from Pongola weather station for Pongola Game Reserve (PGR).

Mean monthly maximum temperatures ranged from 31 ºC in December, January and February to 24 ºC in June/July during the study period (Figure 1.3). Mean monthly minimum temperatures are lowest in June/July at 9 ^{o}C. These conditions are conducive to summers being hot and humid while winters are likely to be moderately dry and mild. The high levels of rainfall that occur between September and April, the equitable temperatures that also characterize this period and high levels of solar radiation are conducive to the production of high levels of plant biomass.

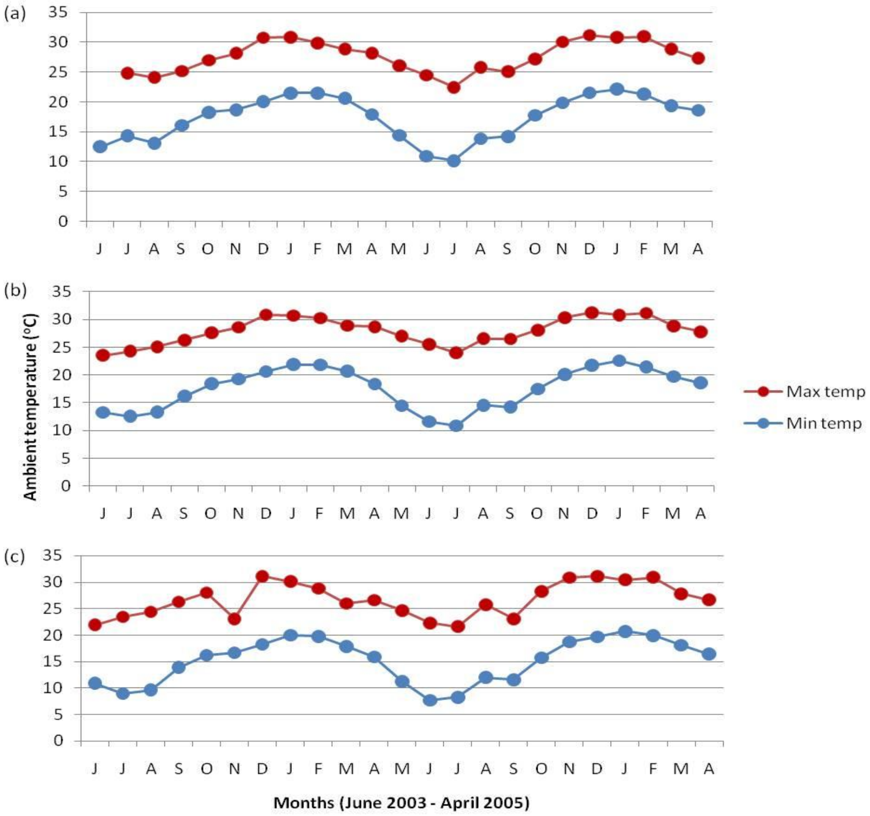

Figure 1.3: Monthly maximum and minimum temperatures for (a) Bonamanzi Game Park (BGP), (b) Mun-Ya-Wana Private Game Reserve (MGR) and (c) Pongola Game Reserve (PGR) for the study period June 2003 to April 2005. Data from Charters Creek weather station for BGP, from Mkuze Game Reserve weather station for MGR and from Pongola weather station for PGR.

Soils

The weathering of rhyolite and basalt on the Lebombo Mountains has produced relatively fertile soils with high clay contents over the entire study area (Matthews 2005). Broad soil groups occurring on PGR include vertic and melanic soils (Fey 2010). These are black and red strongly clayey soils with high base status (Fey 2010). The broad soil groups occurring on BGP and MGR include vertic, melanic, oxidic and cumulic soils. The oxidic soils occurring on BGP and MGR are red and yellow sandy well drained soils with high base status (Fey 2010). The cumulic soils occurring on BGP and MGR are red yellow and greyish soils with low to medium base status (Fey 2010).

Water table, ground water movements and soil moisture retention all play an important role in vegetation growth and maintenance (Matthews 2005). The water table varies from the surface (the study area within BGP during the height of the rainy season) to depths of 60 m or more below the ground surface (Matthews 2005).

Table 1.2: Chemical and physical topsoil properties for Bonamanzi Game Park (BGP), Mun-Ya-Wana Private Game Reserve (MGR) and Pongola Game Reserve (PGR).

	BGP	**MGR**	**PGR**
Phosphorus (mg/L)	2.67	3.00	1.00
Potassium (mg/L)	154.28	217.08	346.80
Calcium (mg/L)	1173.33	948.00	3775.00
Organic carbon (%)	0.00	0.62	0.00
Clay (%)	30.30	18.96	50.39
Total cations ($cmol_c$/L)	16.63	9.77	35.13
pH (KCl)	5.88	4.95	6.28

Browsers

The 2004 game census recording 12 species of ungulates occurring on BGR and 13 species (if the definition of ungulate is expanded to include elephant and rhino) on both MGR and PGR (Table 1.3). Of that 78% are, to varying degrees, browsers.

Table 1.3: Large herbivore species occurring on each of the study areas (Bonamanzi Game Park (BGP), Mun-Ya-Wana Private Game Reserve (MGR), and Pongola Game Reserve (PGR), their dietary preferences* and the most current census data (2004) at the time of the study.

Species	**Dietary preference**	**2004 Census counts**		
		BGR	**MGR**	**PGR**
Buffalo (*Syncerus caffer*)	Graze	0	137	0
Bushbuck (*Tragelaphus scriptus*)	Predominantly browse	30	0	58
Duiker, Grey (*Sylvicapra grimmia*)	Browse	5	6	68
Duiker, Red (*Cephalophus natalensis*)	Browse	34	28	44
Elephant (*Loxodonta africana*)	Mixed	4	41	0
Giraffe (*Giraffa camelopardalis*)	Predominantly browse	9	105	62
Impala (*Aepyceros melampus*)	Mixed	299	1480	4327
Kudu (*Tragelaphus strepsiceros*)	Predominantly browse	33	187	225
Nyala (*Tragelaphus angasi*)	Predominantly browse	507	1063	428
Reedbuck (*Redunca arundinum*)	Predominantly graze	79	19	108
Rhino, White (*Ceratotherium simum*)	Graze	0	86	16
Steenbok (*Raphicerus campestris*)	Mixed	0	0	32
Waterbuck (*Kobus elypsiprimnus*)	Predominantly graze	36	0	100
Wildebeest, Blue (*Connochaetes taurinus*)	Graze	238	379	752
Zebra, Burchell's (*Equus burchelli*)	Predominantly graze	35	229	293

* Dietary preferences taken from Skinner and Smithers (1990).

Thesis outline

Each chapter of this thesis, except for the introduction and the synthesis, has been written as an individual paper, and can be read independently of the rest of the thesis. All chapters are to be submitted as research papers to peer-reviewed journals. Consequently, an overlap occurs in the introductions and descriptions of methods of the different chapters.

Chapter 2:

Most studies aimed to quantify the forage resource of various browse species are over 30 years old, suggesting that the topic of browse availability, apart from the development of the BECVOL model, has been allowed to lapse. With the increase of game farming in woody areas, however, it has become an important subject to revisit and revise. The aim of this component of this study was to refine a method for estimating available browse biomass based on the regression analysis between the canopy volume of a tree and its true leaf dry mass. They should also provide a more objective means of determining the browsing capacity of a tree population, should the browse requirement of a browser be known, as well as the availability of browse during the year as influenced by the seasons.

Chapters 3, 4 and 6:

The accurate prediction of browse production is considered to be of value to any management system, whether conservation, game ranching or even game farming, as it allows for some degree of monitoring to take place and for estimates of game carrying capacities to be determined. A plant's ability to recover from a loss of new shoots differs between species as well as the intensity and frequency of defoliation. This is an important management concern, especially since mammalian browsers, being highly selective feeders, show marked preference for certain key species, tending to leave almost untouched less 'palatable' species. The aim of this component of this study was to measure the browse production of seven key savanna tree species, common along the northern Zululand coast of KwaZulu-Natal, and to investigate factors influencing the rate and quantity of browse production of these species. Furthermore, I aimed to determine which factors can best be used to predict browse production over the growing season.

Chapter 5:

The aim of this chapter was to primarily investigate the relation between the palatability and nutritive value of six key savanna tree species, common along the northern Zululand coast of KwaZulu-Natal, and in turn relate these findings to the annual browse production of these species. The investigation of these questions should develop our understanding of the dynamics of browse production and browser selection among woody plants in semi-arid, South African savannas, assisting the modelling of browse-browser interactions needed to determine browser carrying capacities, as well as evaluating impacts of browsing animals on vegetation.

Chapter 7:

Finally, in Chapter 7, I synthesised what was learned about the production of browse (shoots and leaves) in semi-arid savanna. Referring to related published work, I have, in this chapter, placed the findings of this study in the broader context of determining browser carrying capacity. Lastly, the implications for the management of savannas were discussed.

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CHAPTER 2. LEAF DRY MASS ESTIMATION OF WOODY PLANTS IN NORTHERN ZULULAND

“If it can't be expressed in figures,
it is not science; it is opinion.”
Robert Heinlein

Abstract

The increase of game ranching in savannas has necessitated the need for a greater understanding of browsing capacity. Subsequently, it has become necessary to revisit and refine techniques used to estimate woody plant biomass, in particular available browse biomass for large browsing herbivores. This study investigated the relation between leaf dry mass (LDM) and measurable tree dimensions in order to estimate the available browse biomass of four key savanna tree species, common along the northern Zululand coast of KwaZulu-Natal. A procedure is described for obtaining allometric regression equations to estimate non-destructively and in a cost-effective manner the current year's available browse biomass for the four key savanna tree species, during the dormant season.

Non-linear regression was used to investigate the relation between the leaf dry mass (LDM) of deciduous *Acacia nilotica,* evergreen *Euclea divinorum* and *Gymnosporia senegalensis* and semi-deciduous *Spirostachys africana* and their respective canopy volumes (CVol). Exponential regression ($y = a + br^{\ln x}$) of the natural logarithm of CVol data provided the most accurate and precise description of the tree CVol – LDM relation. Significant relations were obtained over a 2-year period (2003-2004) for species – site models and general species models. The introduction of the calculation of partial volumes enabled the estimation of available browse volumes below certain herbivore feeding levels. The incorporation of tree foliage densities in LDM estimation further improved model accuracy and precision.

The resultant species models are a useful tool in the management and monitoring of available leaf material over a period. They provide an objective means of determining the browsing capacity of a tree population, should the browse requirement of a browser be known.

Introduction

The determination of the carrying capacity of game ranch systems has been the subject of much debate (Walker 1976, Falkena and van Hoven 2000, Dekker 1997, Bezuidenhout 2005, Mentis and Duke 1976, Dhondt 1988, Fritz and

Duncan 1994, Furstenburg 2002). The population density of herbivores is ultimately limited by the availability of their forage resources (Pellew 1981, Pietersen et al. 1993), whilst the sustainability of a herbivore population in any conservation or game ranching system is limited by the sustainability of the vegetation. In seasonally variable environments the supply of dry-season forage determines the numbers of ungulates that can be carried (Mukungurutse 2002). Browse is a major constituent of most ungulate diets throughout the year, but is especially important during the dry season (particularly during droughts) (Mukungurutse 2002). Although browse is a significant and comparatively (cf grasses) dependable component of forage resources, the assessment of its productive capacity for livestock and wildlife had been hampered by the limited knowledge of browse production, its seasonality, its response to climatic variations, and its acceptability to and proportion utilisable by different classes of ungulates. The quantification of browse biomass in southern African savanna systems has received some attention (Pitt and Schwab 1990, Smit 1996, Cissé 1980, Rutherford 1979, Walker 1980), but relating browse biomass to browsing capacity determination needs further input.

The development of regression equations relating various plant dimensions, such as tree height, diameter of the main stem or stems, and area or volume of the leaf canopy, to the amount of potentially edible material (available biomass), is a technique which has proved successful with a wide variety of plants under a wide range of conditions (Barnes 1976, Rutherford 1979). Several studies have reported stem diameter being highly correlated with leaf dry mass (LDM) (e.g. Schuster 1965, Rutherford 1979). Since all the nutrients and water required in leaf production, maintenance, and growth have to pass through the plant stem, intuitively, a strong positive relation should exist between LDM and stem diameter. Larger stems should, therefore, be able to support a larger leaf mass. Rutherford (1979) reported 12 equations for browse biomass estimation for different tree species, using stem diameter, or a combination of stem diameter and tree height as the explanatory variables. Examples of tree species, for which such relations have been defined include: *Colophospermum mopane* (Barnes et al. 1976), *Sclerocarya caffra* (Kelly and Walker 1976), *Burkea africana* (Rutherford 1979), and *Terminalia sericea* (Rutherford 1979). The use of a single measured variable as a predictor of LDM considerably reduces the amount of field data collection required, providing a quick and relatively easy method of available browse biomass determination.

Most contemporary models for predicting browsing capacity base estimations of available browse on the canopy volume (CVol) of woody species (Melville et al. 1999). The most widely recognised browse prediction model in southern Africa is the BECVOL (Biomass Estimates from Canopy VOLume) model developed by Smit (1989a). This method enables the user to calculate the canopy volume of various tree species through the measurement of seven tree dimensions. The estimation of the browsing capacity is then based on those measurements. A relation has been demonstrated between canopy volume and leaf dry mass (Smit 1989b). It can therefore be anticipated that a relation exists between canopy volume and browse availability (Melville et al. 1999).

Apart from recent remote sensing work (Wu et al. 2009, Colgan et al. 2012), most direct studies aimed to quantify the forage resource of various browse species are over 30 years old, suggesting that the topic of browse availability, apart from BECVOL, has been allowed to lapse. With the increase of game farming in woody areas, however, it has become an important subject to revisit and refine. This study was initiated with the primary aim of developing a revised regression analysis method for estimating available browse biomass of four key savanna tree species, common along the northern Zululand coast of KwaZulu-Natal. It was hypothesized that available browse biomass (measured as LDM in this study) may be accurately estimated from measurable tree dimensions, particularly dimensions relating to the tree canopy bounds. My specific objectives were: (a) to develop a reliable method to calculate the CVol of a tree where fewer than seven field measurements, as used in BECVOL, are required to obtain such estimates; (b) determine which of measured and calculated tree dimensions (tree height, height to the lowest leaves, average canopy diameter, stem diameter and CVol) best predicts LDM, with the prediction that CVol, being a combination of a number of variables relating to tree canopy size, would best predict LDM (c) to develop regression equations for each of the four savanna tree species for each study area, with the prediction that regression analysis would reveal that estimates of LDM would differ across study areas, based on rainfall; (d) to develop general species models accounting for the variation across study areas which may be used in the field to estimate total browse availability, with the prediction that the resultant models may be used to determine stocking rates, assess impacts of browsing on browseable vegetation and monitor browsing trends over time.

Procedure

Study areas

Data were collected in the open wooded grassland areas of three game reserves in north eastern KwaZulu-Natal: Bonamanzi Game Park (BGP), Mun-Ya-Wana Private Game Reserve (MGR), and Pongola Game Reserve (North) (PGR). The three study areas are situated on an approximately north/ south axis along the northern Zululand coastline and are situated along a distinct rainfall and temperature gradient (Figure 1.1). These differences allow for estimations of browse availability across a range of environmental conditions and provide an opportunity to observe the influence of such conditions on browse availability.

The study was conducted over two years (2003-2004) during the winter season (July) because, in terms of forage availability, the winter season is the most limiting period of the year for available browse and therefore the period of the year during which the carrying capacity of a given area is likely to be at its lowest.

Data collection

Selection of tree species

Browse availability estimates were based on four key tree species, *Acacia nilotica, Euclea divinorum, Gymnosporia senegalensis* and *Spirostachys africana.* These species were chosen because they represent a range of palatability and leaf sizes (Table 2.1), were common, and occurred at high densities across all three study areas.

Table 2.1: A comparison of palatability, leaf size and tree guild of the four study tree species.

	A. nilotica	***E. divinorum***	***G. senegalensis***	***S. africana***
Palatability	Favoured [2,3,4]	Not favoured [1,2,4]	Moderately favoured[4,5,7]	Highly favoured[3,4,6]
Ave leaf size (mm)	2.5 [3] (leaflet size)	57.5 x 17.5 [3]	50 x 30 [3]	40 x 20 [4]
Leaf category*	Microphyllus[3]	Macrophyllus[3]	Macrophyllus[3]	Mesophyllus[3]
Tree guild	Deciduous[3]	Evergreen[3]	Evergreen[3]	Semi-deciduous[3]

*Macrophyllus – having large or elongated leaves with usually many veins or a much branched vein (>60x20 mm)

*Mesophyllus – as for macrophyllous (<60x20 mm)

*Microphyllus – have small leaves with a single unbranched vein (<30x10 mm)

1 (Bowland 1990)

2 (Owen-Smith 1979)

3 (Owen-Smith and Cooper 1987a)

4 (Pooley 1997)

5 (Rauff 2002)

6 (Sauer et al. 1977)

7 (Smits 1986)

8 (Tello and van Gelder 1975)

9 (Watson and Owen-Smith 2002)

Sixteen individual plants of each of the four study tree species in each of the three study areas were selected for harvesting. The selected individuals included a range of size classes representative of the population (except seedlings). The following dimensions were measured on each individual tree prior to harvesting the leaves: (a) tree height (HT) (m), (b) height of first leaves or potential leaf bearing stems (HL) (m), (c) average canopy diameter (D) (m), and (d) stem diameter (Stem D) (m) (measured 0.5 m above ground level). Prior to harvesting, each individual was subjectively allocated to a foliage density (FD) category by visual assessment. Foliage density classes were defined as follows (adapted from Pellew (1981b)): 0: no green leaf at all; tree in deciduous phase, 1: 20% lateral obscurity, canopy leaf cover sparse, 2: 40% lateral obscurity, canopy leaf cover relatively sparse, 3: 60% lateral obscurity, canopy leaf cover moderately dense, 4: 80% lateral obscurity, canopy leaf cover dense, 5: 100% lateral obscurity, canopy leaf cover solid and very dense. A collection of reference photographs was compiled of the four tree species and their different foliage density classes. A representative sample of leaves (between 20-50% of the canopy depending on the tree size), from each tree, was separated by hand from twigs and stems, and was dried to a constant mass in a drying oven (70^{o}C) and weighed.

Data analysis

Calculation of canopy volume and partial volumes

Due to the variability in tree spatial canopy shape, with different tree sizes, maturities, species and under differing levels of browse intensity, the CVol of each study tree was calculated from the dimension measurements (a – c above) by using the volume formula of an ellipse (Equation 2.1). This approach was developed because of a lack of any suitable existing approach. An ellipse was chosen as most macrophyllous trees, at maturity approximate this shape, while most microphyllous species, under browsing also become more spherical in shape.

Equation 2.1

$$V = \frac{4}{3}\pi r^3$$

Equation 2.2

$$r = \frac{\left(\frac{HT - HL}{2}\right) + \left(\frac{D}{2}\right)}{2}$$

Where:

V = volume (m^3)

r = average tree canopy radius (m) (Figure 2.1)

HT = tree height (m) (Figure 2.1)

HL = height of first leaves or potential leaf bearing stems (m) (Figure 2.1)

D = average canopy diameter (m)

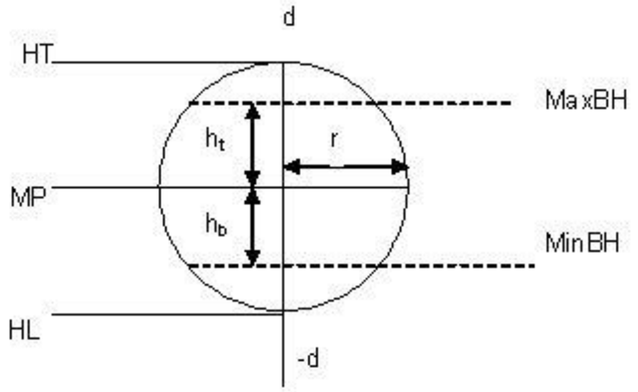


Figure 2.1: Schematic illustration of a stylised tree, its measurements and structure. Where: r = average tree canopy radius (m); HT = tree height (m); HL = height of first leaves or potential leaf bearing stems (m); MP = the midpoint of the tree canopy; h_b= height above/below the midpoint of the tree canopy relating to the minimum browse height (adjusted depending on the species of interest) (m); h_t = height above/below the midpoint of the tree canopy relating to the maximum browse height (adjusted depending on the species of interest) (m); d= the distance from the midpoint of the canopy to HT; -d = the distance from the midpoint of the canopy to HL, MaxBH = maximum browse height (m) and MinBH = minimum browse height (m).

In order to calculate leaf mass of a tree below any specified maximum browse height (MaxBH) or, above any minimum browse height (MinBH), the calculation of partial volumes is used. Partial volumes were calculated when determining the available browse biomass for ungulates with specific feeding levels, for example, impala cannot browse above 2 m (du Toit 1990) while giraffe do not tend to browse below 1 m (Owen-Smith 1988). The calculation of partial volumes uses the integration of a series of circles, allowing for a wider range of tree shapes to be included. The general equation to calculate the partial volume of a tree canopy with defined maximum and minimum browse heights is described in Equation 2.3 below:

Equation 2.3

$$V = \pi r^2 \left[h_b - \frac{(h_b)^3}{3d^2} - h_t + \frac{(h_t)^3}{3d^2} \right]$$

Where:

V = CV (m^3)

πr^2 = circle area (m^2)

MP = the midpoint of the tree canopy (Figure 2.1)

Equation 2.4

$$MP = \frac{HT - HL}{2} + HL$$

h_b = height above/below the midpoint of the tree canopy relating to the minimum browse height (adjusted depending on the species of interest) (m) (Figure 2.1)

h_t = height above/below the midpoint of the tree canopy relating to the maximum browse height (adjusted depending on the species of interest) (m) (Figure 2.1)

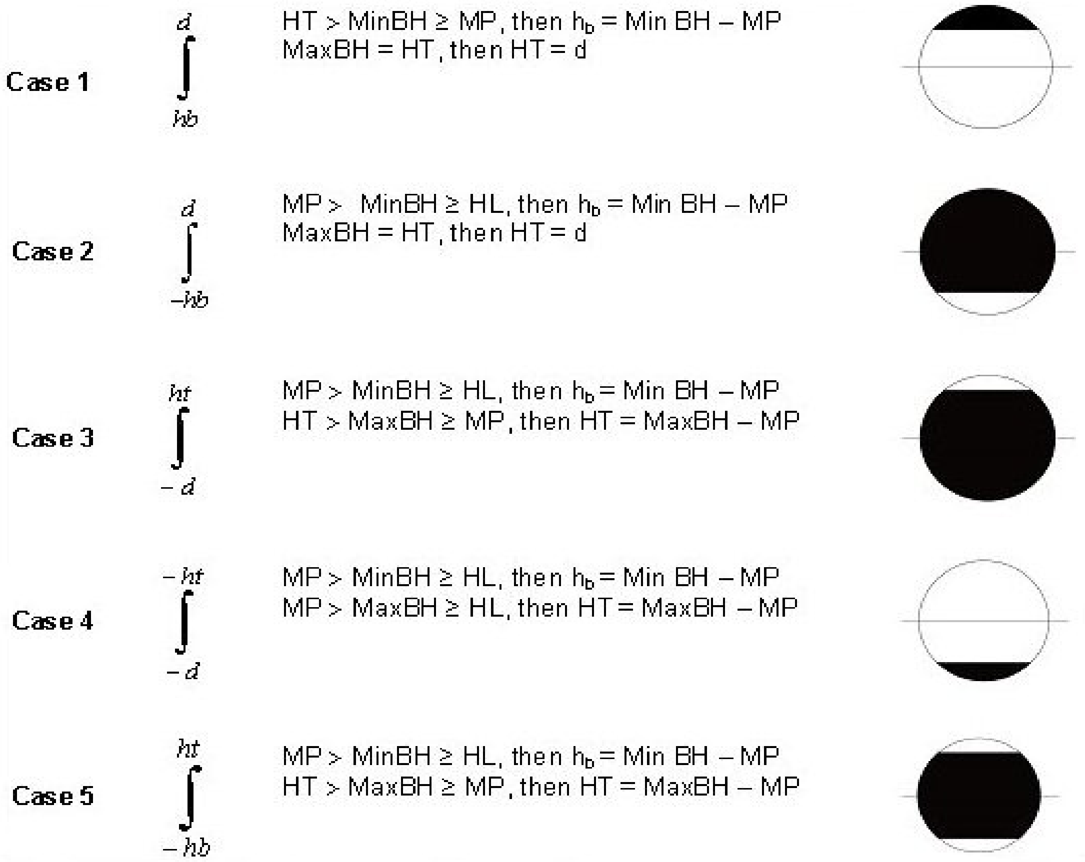
d = the distance from the midpoint of the canopy to HT (Figure 2.1)

-d = the distance from the midpoint of the canopy to HL (Figure 2.1)

Equation 2.5

$$d = (HT - HL) \times 0.5$$

We recognise ten main possibilities in the calculation of partial volumes, each requiring a separate integration formula:



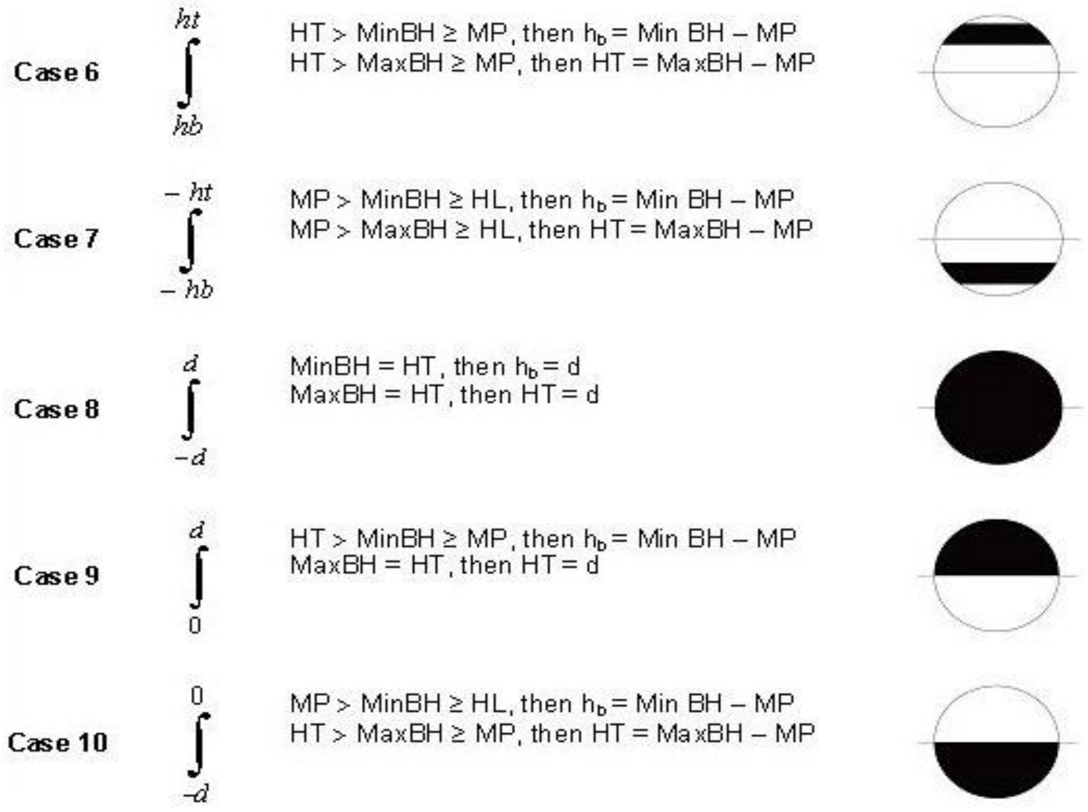
Case 1 $\int_{hb}^{d}$ HT > MinBH ≥ MP, then h_b = Min BH – MP
MaxBH = HT, then HT = d

Case 2 $\int_{-hb}^{d}$ MP > MinBH ≥ HL, then h_b = Min BH – MP
MaxBH = HT, then HT = d

Case 3 $\int_{-d}^{ht}$ MP > MinBH ≥ HL, then h_b = Min BH – MP
HT > MaxBH ≥ MP, then HT = MaxBH – MP

Case 4 $\int_{-d}^{-ht}$ MP > MinBH ≥ HL, then h_b = Min BH – MP
MP > MaxBH ≥ HL, then HT = MaxBH – MP

Case 5 $\int_{-hb}^{ht}$ MP > MinBH ≥ HL, then h_b = Min BH – MP
HT > MaxBH ≥ MP, then HT = MaxBH – MP



Case 6	$\int_{hb}^{ht}$	HT > MinBH ≥ MP, then h_b = Min BH – MP HT > MaxBH ≥ MP, then HT = MaxBH – MP
Case 7	$\int_{-hb}^{-ht}$	MP > MinBH ≥ HL, then h_b = Min BH – MP MP > MaxBH ≥ HL, then HT = MaxBH – MP
Case 8	$\int_{-d}^{d}$	MinBH = HT, then h_b = d MaxBH = HT, then HT = d
Case 9	$\int_{0}^{d}$	HT > MinBH ≥ MP, then h_b = Min BH – MP MaxBH = HT, then HT = d
Case 10	$\int_{-d}^{0}$	MP > MinBH ≥ HL, then h_b = Min BH – MP HT > MaxBH ≥ MP, then HT = MaxBH – MP

Variable correlations

Correlation matrices were drawn up using all of the measured tree dimensions described in 'Data collection' together with the LDMs and calculated CVols of all individuals. Correlation matrices reflect indices of association between variables (McConway et al. 1999). The strength of these associations is measured by the *Pearson product-moment correlation coefficient* (r):

Equation 2.6

$$r = \frac{\frac{1}{n-1}\sum_{i=1}^{n}(x_i - \bar{x})(y_i - \bar{y})}{s_x s_y}$$

The correlation coefficient (r) is bound between +1 and –1, where values close to +1 are highly positively correlated and values close to –1 are highly negatively correlated, with zero indicating no correlation (McConway et al. 1999).

For the purposes of this study, the variables with the strongest positive correlations to LDM would be recognised as the best explanatory variables for predicting available browse biomass.

Regression analysis

Populations with a small CVol range generally appear linear in relation to LDM (Smit 1989a), but in those with larger CVol ranges the relation becomes markedly curvilinear (Rutherford 1979, King 1975). The curvilinearity of the relations may indicate that with increasing canopy size, there are fewer leaves per unit volume. In most savanna tree species the leaves are concentrated at the outer perimeter of the canopy and with increasing tree size an increasingly large area in the centre of the canopy doesn't have any leaves (Van der Meulen and Werger 1984).

Non-linear regression (exponential models) (Genstat 9.1.0.147, Lawes Agricultural 2006) was used to relate true LDM (dependent variable) to calculated CVol (independent variable). The transformation of the CVols (on the x-axis) to their natural logarithmic values was applied in an attempt to reduce heteroscedasticity, where variance increases with increasing values of the independent variable (Baskerville 1972). In most cases logarithmic transformations were done to obtain linearity of non-linear data (Rutherford 1979). This partial transformation did not alter the curvilinearity of the plotted lines, but merely changed them from being convex to concave (Smit 1996). In this form the data were well suited for fitting the exponential regression equation ($y = a + b*r^{\ln x}$), where the natural logarithmic values of *x* were used. By resorting to a partial logarithmic transformation only, the problem of biased estimates by simply taking antilogarithms of values from a log-log regression line or regression function (Beauchamp and Olson 1973) was largely avoided.

Factors considered when selecting from the several resultant non-nested models included ecological feasibility and accuracy (Bates and Watts 1988). Thereafter, other factors of importance were: (a) model simplicity (a simpler model is always preferred over a more complex one); (b) a high correlation coefficient (parameter estimates should provide an adequate fit of the model to the data); (c) a random residual plot; and (d) small residual mean square (Bates and Watts 1988).

In addition to considering factors (a) - (d), model accuracy was assessed according to the closeness of the fit of the plot of fitted values overlaid with observed values (Bates and Watts 1988); and the deviation of the mean of the observed dependent variable from the mean of predicted values (MacCracken and van Ballenberghe 1993b). Accuracy of 10% and less was considered desirable, while an accuracy of 11-25% was considered acceptable (Simpson et al. 2004).

Concurrent line tests

Concurrent line tests were done on each combination of study areas, for each of the four tree species, to determine the amount of deviation between the two separate regression equations developed for each individual study area. Concurrent line tests help to explain the variation between study areas, the degree of variation and provide information as to where the most amount of variation occurs (i.e. the slope or the intercept) (Crowder 1978). Essentially, concurrent line tests determine the amount of additional variation explained by fitting two lines instead of one. If this variation is highly significant, a joint fit cannot be accurately used to analyse two datasets (Crowder 1978).

Corrected LDMs

A common tendency in sampling for drawing up a relation is to select vigorously growing trees of good form, which results in overestimation of productivity when regressions from these data are applied to fixed transect data (Whittaker and Marks 1975, cited by Rutherford 1979). One way to overcome this problem is to stratify the samples used in defining a relation (Rutherford 1979). In this study, stratification took the form of foliage density classes (defined in ‘Data collection). Hutchings and Mason (1970) successfully stratified gambel oak trees in different foliage density classes prior to regression determination. Trees representative of all five foliage density classes (for each species), and a range of tree heights and average canopy diameters were sampled. An inescapable consequence of this, however, is a reduced goodness of fit and lower correlation in the resulting relation (Rutherford 1979) (Table 2.2). To improve the reduced goodness of fit, the true LDMs of all samples in a foliage density class lower than five, were converted to an estimated LDM for a foliage density of five, through a simple ratio conversion. For example, if an individual was assigned a foliage density of 3, and had a true leaf dry mass of 3.5 kg, the estimated leaf dry mass for that individual with a foliage density of 5 would be (3.5 kg/3)*5 = 5.8 kg. This allowed for comparisons of LDM for a range of CVols on the same scale, without necessitating laborious sampling and the derivation of a unique equation for each foliage density class. Foliage density (FD) was factored into the resulting general regression equation for each of the four tree species, to allow for the estimation of LDMs of trees in foliage density classes lower than five post calculation. The resulting general equation is as follows:

Equation 2.7

$$Y = \frac{FD}{5}(a + br^{lnX})$$

Where:

Y	= LDM (kg)
FD	= assigned foliage density class of the individual
a,b and r	= coefficients
X	= calculated CVol (ln m^3)

Table 2.2: Correlation coefficients, showing the strengths of the associations between the corrected and uncorrected LDMs and calculated CVol for each of the four tree species across all three study areas.

Species	**Correlation with CVol**	
	Corrected LDM	**Uncorrected LDM**
A. nilotica	0.94	0.92
E. divinorum	0.94	0.83
G. senegalensis	0.96	0.92
S. africana	0.74	0.69

Results

Variable correlations

Correlation matrices derived for each of the four tree species, across all study areas, consistently indicated higher correlations between LDM and the calculated CVol, than between LDM and the measured tree dimensions (Table 2.3).

For this study, stem diameter was discarded as a predictor variable due to the inconsistency in the correlations between stem diameter and LDM within a species and between species (Table 2.3). Where individuals of a species comprise multiple stems, the correlation between stem diameter and leaf dry mass is poor, as in the case of *G. senegalensis* in BGP, where the correlation of leaf dry mass with stem diameter was 0.08.

Table 2.3: Correlation coefficients, showing the strengths of the associations between leaf dry mass (LDM) and the measured and calculated tree dimensions for the four tree species across three study areas (HT = tree height, HL = height to lowest leaves, D = average canopy diameter, CVol = canopy volume and Stem D = stem diameter at 0.5m).

Species	**Study area**	**Correlation with LDM**				
		Ht (m)	**HL (m)**	**D (m)**	**CVol (m^3)**	**Stem D (m)**
A. nilotica	BGP	0.93	-0.32	0.79	0.96	0.97
	PRR	0.64	-0.05	0.94	0.99	0.65
E. divinorum	BGP	0.87	0.18	0.96	0.97	0.67
	PRR	0.86	0.03	0.83	0.96	0.94
	PGR	0.97	0.57	0.91	0.94	0.88
	Combined	0.72	0.11	0.82	0.76	0.67
G. senegalensis	BGP	0.88	-0.27	0.81	0.98	0.08
	PRR	0.58	0.22	0.60	0.97	0.85
	PGR	0.80	-0.37	0.81	0.98	0.92
	Combined	0.72	-0.12	0.70	0.96	0.86
S. africana	BGP	0.92	-0.14	0.90	0.92	0.89
	PRR	0.94	0.47	0.89	0.96	0.73
	PGR	0.91	0.19	0.87	0.93	0.76
	Combined	0.79	0.30	0.88	0.74	0.58

Derivation of regression equations

Positive curvilinear relations between true LDM and CVol were established for all four harvested tree species across all study areas. Highly significant regressions ($P < 0.001$) with coefficients of determinations exceeding 87% were achieved (Table 2.4, Figure 2.2, Figure 2.3). No regression was established for *A. nilotica* on PGR as in both the dry season of 2003 and 2004, the trees were completely leafless.

The smaller range of CVols used in the MGR regression model for *A. nilotica* was also due to the lack of larger trees that had retained their canopy during sampling in the dry season.

Table 2.4: Regression analysis ($Y = a + br^{\ln X}$) for the four study trees species over two winters (2003-2004), in three study areas along the northern Zululand coastline of KwaZulu-Natal, where Y = LDM (kg) and X = calculated CVol (ln m^3).

Species	**Study site**	**Coefficient**			**n**	**r^2**	***P***	**Accuracy* (% deviation)**
		a	**b**	**r**				
A. nilotica	BGP	0.01	0.46	1.75	16	96.6	<0.001	9.36
	MGR	-0.10	0.39	1.95	16	92.2	<0.001	-8.92
E. divinorum	BGP	0.15	0.89	2.25	16	90.0	<0.001	-16.87
	MGR	-0.16	0.88	1.83	16	96.2	<0.001	-13.36
	PGR	-0.30	0.87	1.52	16	91.8	<0.001	12.85
G. senegalensis	BGP	0.44	0.16	2.85	16	93.9	<0.001	10.85
	MGR	0.67	0.05	4.06	16	87.1	<0.001	12.70
	PGR	0.21	0.31	1.84	16	89.8	<0.001	-16.15
S. africana	BGP	-0.41	0.63	1.47	16	93.7	<0.001	-10.90
	MGR	0.29	0.01	3.75	16	92.6	<0.001	18.44
	PGR	-0.02	0.16	1.77	16	89.5	<0.001	-17.69

*$\left(\left[(Y_O - Y_P)/n\right]/\bar{Y}_O\right)\times 100$

Combining regression models

Species models

Concurrent lines were established for all four tree species for all combinations of study areas (Table 2.5). The BGP model for all of the four tree species consistently recorded higher LDMs per unit CVol (natural logarithmic conversion), at CVols lower than 3, than the MGR and PGR models (Figure 2.4). In deciduous (*A. nilotica*) and semi-deciduous (*S. africana*) trees, the MGR model recorded higher LDMs per unit CVol at CVols above 3 ln m^3 (Figure 2.4a and d respectively).

Table 2.5: Concurrent line tests (H_0: $\text{intercept}_1 = \text{intercept}_2$; $\text{slope}_1 = \text{slope}_2$) for each combination of study areas for each tree species (NS indicates a non significant result, * indicates a significant result at the 95% confidence level, ** indicates a highly significant result at the 99% confidence level).

Species	**Study areas**	**df^1**	**F_{calc}**	**F_{table}**	**Significance**
A. nilotica	BGP and MGR	3,29	0.69	2.93	NS
E. divinorum	BGP and MGR	3,29	0.77	2.93	NS
	MGR and PGR	3,29	0.34	2.93	NS
	PGR and BGP	3,29	2.46	2.93	NS
G. senegalensis	BGP and MGR	3,29	0.00	2.93	NS
	MGR and PGR	3,29	1.27	2.93	NS
	PGR and BGP	3,29	1.23	2.93	NS
S. africana	BGP and MGR	3,29	0.28	2.93	NS
	MGR and PGR	3,29	0.18	2.93	NS
	PGR and BGP	3,29	1.30	2.93	NS

[1](difference between combined model and separate models, combined model)

Failure to achieve highly significant results in the concurrent line tests for any of the tree species (Table 2.5) provided sufficient support for the development of a single non-linear regression model per species across all three study areas. Highly significant regressions (*P* < 0.001) with coefficients of determination exceeding 60% were achieved (Table 2.6, Figure 2.5). The lower accuracies reported for *E. divinorum, G. senegalensis* and *S. africana* (Table 2.6) are highly correlated with the differences in the separate study area models for these species (Figure 2.4).

Table 2.6: Regression analysis ($Y = a + br^{\ln X}$) for the four study trees species over two winters (2003-2004), along the northern Zululand coastline of KwaZulu-Natal, where Y = LDM (kg) and X = calculated CVol (ln m^3).

Species	**Coefficient**			**n**	**r^2**	***P***	**Accuracy***
	a	**b**	**r**				**(% deviation)**
A. nilotica	-0.13	0.51	1.72	32	96.6	<0.001	-10.11
E. divinorum	-0.51	1.35	1.57	48	60.1	<0.001	-37.03
G. senegalensis	-1.05	1.47	1.38	48	72.6	<0.001	-23.43
S. africana	-0.38	0.51	1.45	48	76.8	<0.001	26.05

*$\left(\left[(Y_O - Y_P)/n\right]/\overline{Y}_O\right)\times 100$

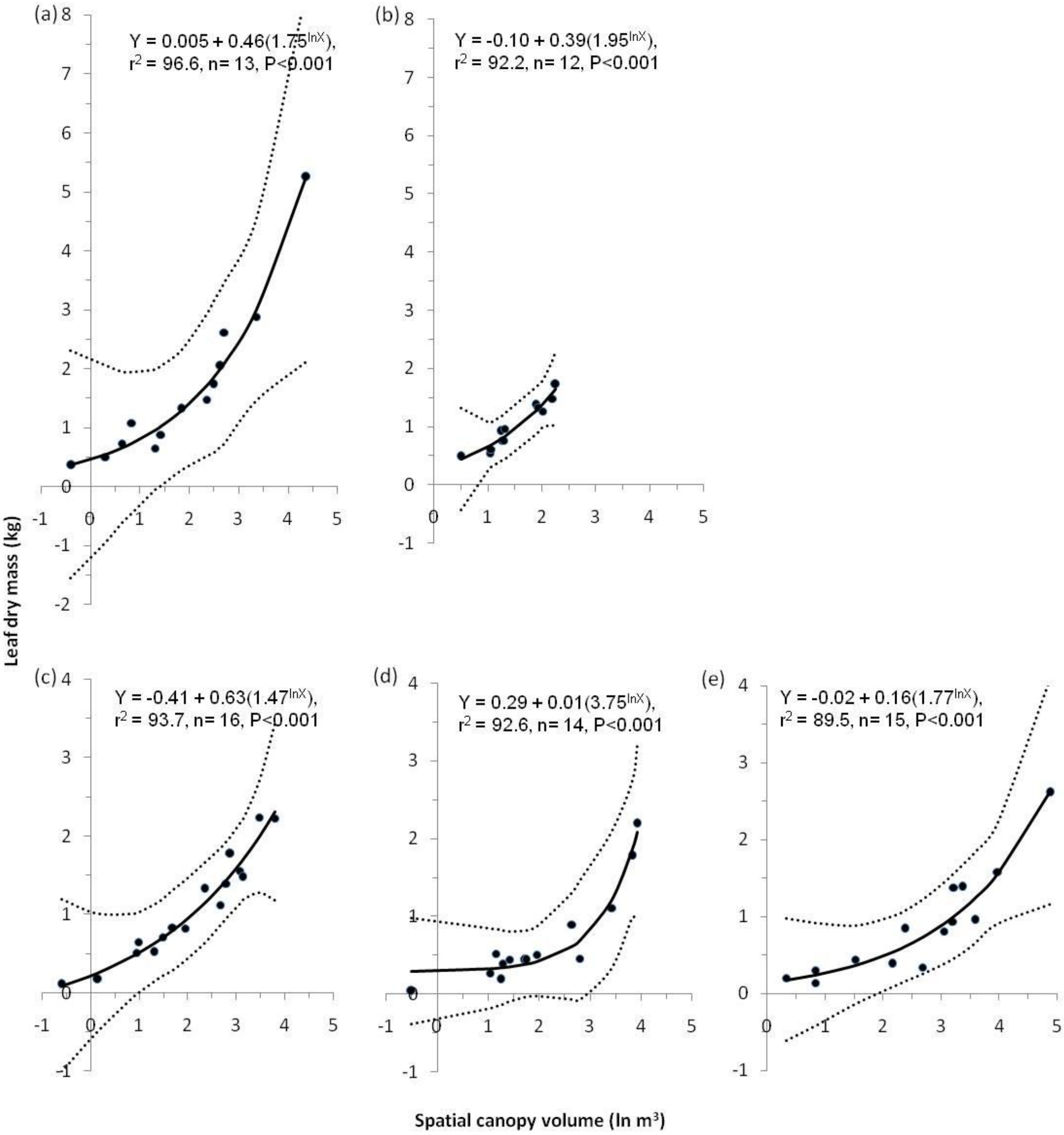


Figure 2.2: Regression analysis of the relation between CVol (natural logarithm conversion) (independent variable) and LDM of *A. nilotica* (a & b) and *S. africana* (c - e) for Bonamanzi Game Park (a & c), Mun-Ya-Wana Private Game Reserve (b & d) and Pongola Game Reserve (e) (dotted lines: 95% confidence limits).

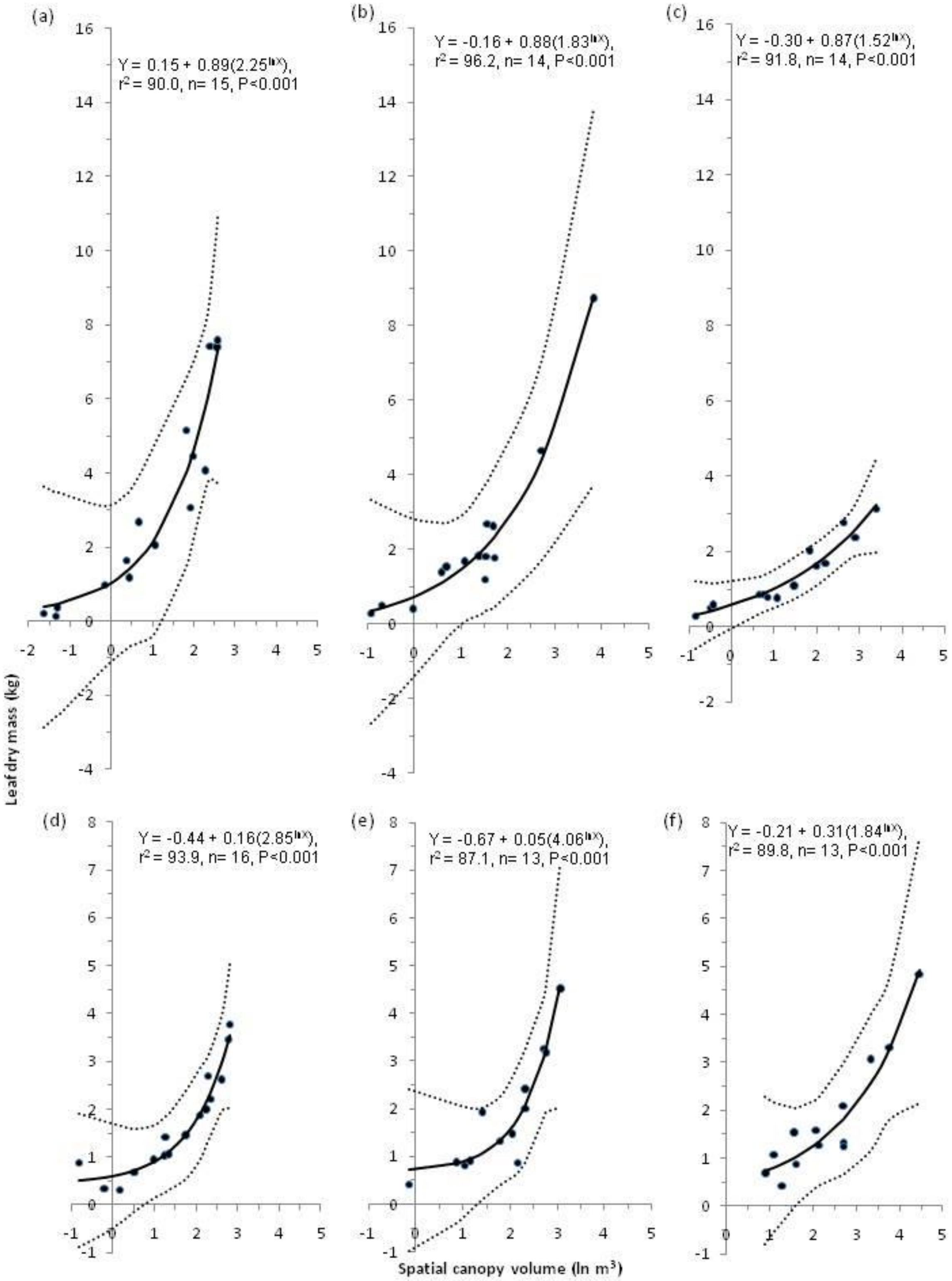


Figure 2.3: Regression analysis of the relation between CVOL (natural logarithm conversion) (independent variable) and LDM of *E. divinorum* (a - c) and *G. senegalensis* (d - f) for Bonamanzi Game Park (a & d), Mun-Ya-Wana Game Reserve (b & e) and Pongola Game Reserve (c & f) (dotted lines: 95% confidence limits).

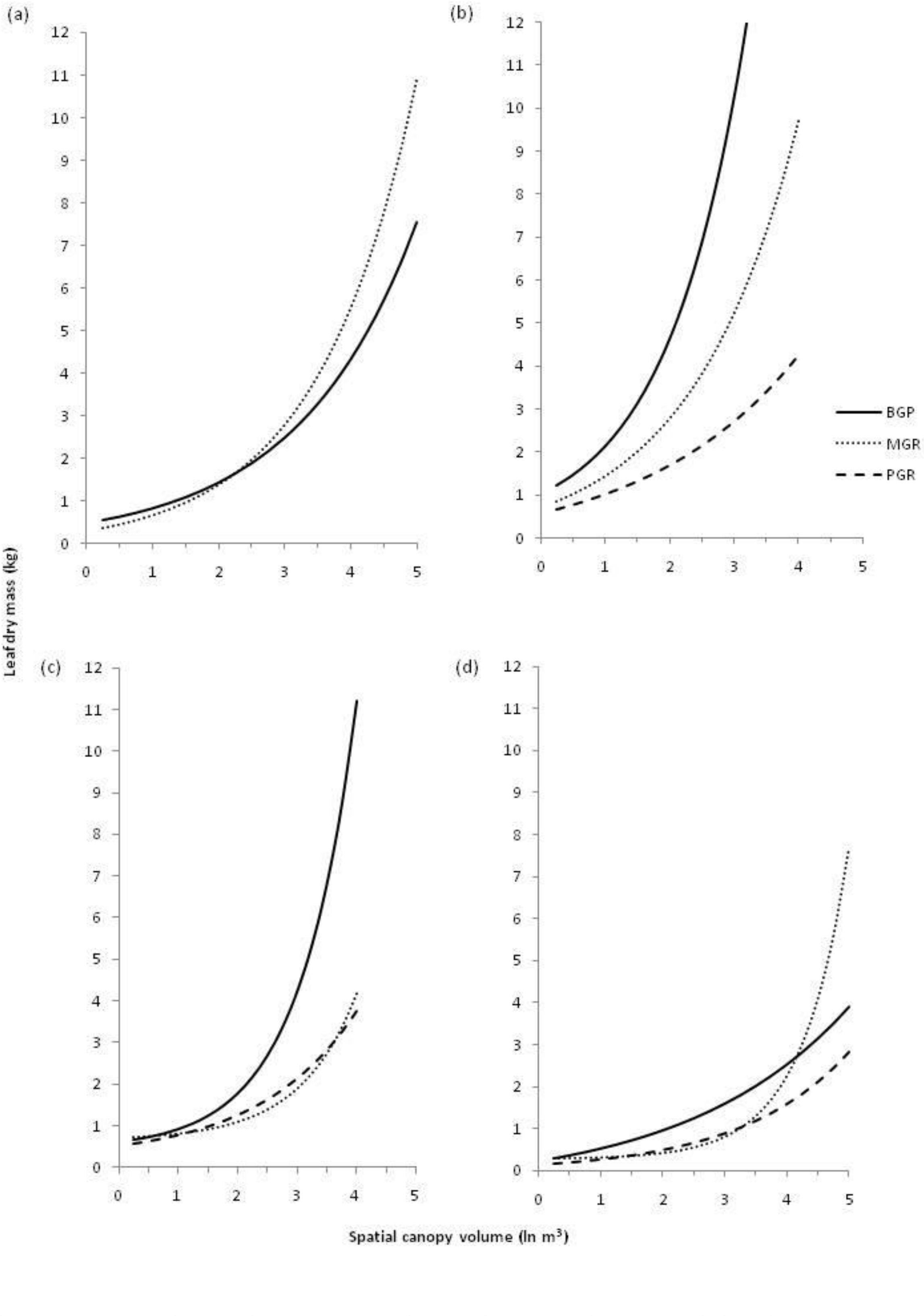


Figure 2.4: Comparison of the separate study area (Bonamanzi Game Park (BGP), Mun-Ya-Wana Private Game Reserve (MGR), Pongola Game Reserve (PGR)) regression analyses (Table 2.4) of the relation between CVol (normal logarithm conversion) (independent variable) and LDM (dependent variable) for (a) *A. nilotica*, (b) *E. divinorum,* (c) *G. senegalensis* and (d) *S. africana.*

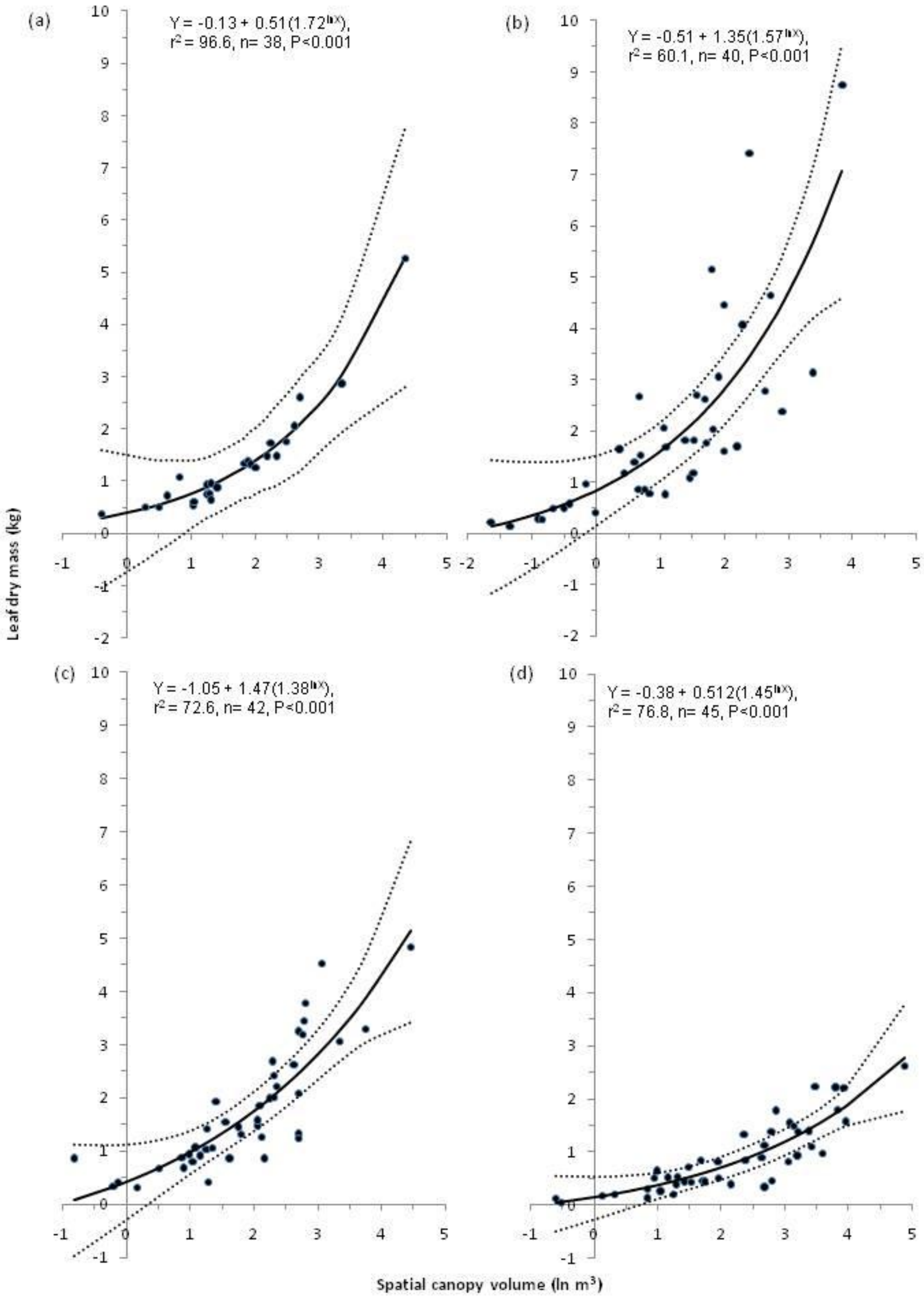


Figure 2.5: Combined regression analysis for all study sites of the relation between CVol (natural logarithm conversion) (independent variable) and LDM of (a) *A. nilotica,* (b) *E. divinorum,* (c) *G. senegalensis* and (d) *S. africana* (dotted lines: 95% confidence limits).

Discussion

Variable correlations

The inconsistent correlations reported between the single measured variables (HT, HL, D and Stem D) and LDM may be attributable to differences in browsing pressure and frequency of burning across the three study areas. Pellew (1981a) reported that stem diameters produced the poorest correlations with the LDM of various *Acacia* species in his study in the Serengeti National Park, and attributed this to the considerable variability of stem diameters in relation to the age of regeneration and the history of burning. He reported that the root-stock of some 2 m tall trees was probably more than 20 years old, the development of the trees being prevented by the combination of browsing and burning. This suggests that tree age, associated with the root-stock volume, has a greater influence on leaf dry mass than stem diameter. Since all the nutrients and water required in leaf production, maintenance, and growth have to pass through the plant stem, a minimum stem diameter that limits LDM may exist, but once that threshold is passed, stem diameter may no longer be a limiting factor. This may be because in larger trees, particularly those that are evergreen, LDM is limited more by competition and shading effects rather than by nutrient and water limitations, although these certainly play a role (Ewel and Mazzarino 2008, Escoto-Rodriguez 2010). The consistently high correlation of calculated CVol with LDM suggests that due to the high variability in tree form and size, no single measurable dimension can reliably be used to predict LDM. Rather, a number of variables, in combination, provide a more accurate estimate. Rittenhouse and Sneva (Rutherford 1979, 1977 cited by) found that there was higher correlation with the LDM of sagebush (*Artemisia tridentate*) when more than one variable was used.

Species regression models

Concurrent lines were established for all four species for all study area combinations. Of the three study areas, BGP had the best conditions for plant growth, in relation to those at MGR and PGR. A comparison of the regression equations for each species for all three study areas reveals that for the most part, LDM on BGP per unit CVol (natural logarithm conversion) is greater than for MGR and PGR, with the general trend being BG*P*>MGR>PGR (especially at lower CVol values).

The difference in study area regressions was greatest in the evergreen species, *G. senegalensis* and *E. divinorum. Gymnosporia* spp. are evergreen trees that are generally more specialized in coping with dry conditions (van Essen et al. 2002). These species also rely on deep rooting and secondary thickening of their leaves to tolerate desiccation. In comparison to deciduous species (like *Acacias*), evergreen species have moderate growth rates, are tall trees, and have a lower digestibility than the deciduous species (Coley 1983). As a result, these species have less potential to respond rapidly to small changes in the favourability of growing conditions, and tend to respond more gradually over time. The small differences in the growing conditions between MGR and PGR therefore had little effect on estimations of LDM, while the improved conditions for growth on BGP resulted in improved LDM estimations per unit CVol.

Euclea divinorum, on the other hand, was the only tree species for which clear differences between the separate study area regressions were established. Although *E. divinorum* is an evergreen species, it is regarded as an invasive species in Zululand due to its capacity for rapid growth and coppicing under favourable conditions (Pooley 1997). *Euclea divinorum* is therefore better able than *G. senegalensis* to respond to favourable conditions, i.e. small improvements in the growing conditions lead to big changes in the actual growth rates of the trees. As a result large differences in LDM, especially at greater CVols, exist between the three study areas. The combined general model for the species has, as a result, lower prediction accuracy.

Acacia nilotica and *S. africana* recorded only very small differences between the separate study area regressions. These species are deciduous and semi-deciduous respectively, and thus generally show high potential growth rates, and have the ability to grow quickly when conditions are favourable (van Essen et al. 2002). With this in mind it might have been expected that differences in study area regressions should have been larger than those recorded for the slower growing evergreen species. The regressions, however, were developed for the dry season, when most (if not all) new growth ceases in deciduous trees and the loss of leaves takes place. While *A. nilotica* has been classified in this study as a deciduous tree, it in fact only reaches true deciduousness on PGR.

Building general regression models for LDM determination

In the management of the woody component of most savanna type ecosystems there is a need to identify the more common tree species. The remaining group of rarer species, however, may sometimes comprise a large number of species for which the drawing up of relations for each is not feasible, yet may be important to managers as a group. Relations determined for the more common species, within a given area may be used for rarer species of similar physical proportions (Brown 1976, Rutherford 1979). Although *A. nilotica, E. divinorum, G. senegalensis* and *S. africana* are common throughout northern Zululand, they are obviously not the only tree species occurring in this area. Determinations of available browse biomass for the northern Zululand region of KwaZulu-Natal would better be predicted using more general equations that encompass all browseable species.

Available browse may be viewed as “the sum total of the plant material of a woody species that is potentially edible to a specified set of animals” (Rutherford 1979). The ability to accurately quantify available browse rests on the ability of any predictive model to take the following factors into account: (a) browse consists of a very large number of small discrete parts, namely twigs, leaves, shoots, buds, fruit and flowers (only LDM was considered in this study); (b) the three-dimensional distribution of these discrete parts on the plant is highly varied; and (c) the spatial distribution of woody plants within a landscape can be highly heterogeneous.

In trying to take all of these factors into account, a trade-off between model simplicity and practicality (in terms of application in the field) and model predictive quality becomes necessary. Generally, due to time and resource constraints, model-simplicity is favoured over model predictive quality. For the purposes of this study, the models defined, as far as possible, account for three-dimensional variability in the distribution of browse on a tree using calculated CVols, rather than single measured variables to explain changes in LDM. Three-dimensional variation was further accounted for by the non-random selection of individuals of all size classes and the stratification of individuals into foliage density classes.

It is necessary to recognise the limitations of any model and to ensure the use of the model within these limits. Regression equations, demonstrated by Rutherford (1979), are restricted to biomass measurements at the time of sampling (or the same time in successive years), and are not suitable for monitoring seasonal changes in a highly variable resource (Pellew 1981). The models reported in this study should, ideally, only be used in the northern Zululand region of KwaZulu-Natal, in areas where environmental conditions such as those for which the models were developed, occur.

An important assumption in the calculation of CVol is that the canopy of all tree species approximates a sphere. Where species with a totally different growth form occur, a separate relation may be required. Individual species treatment is also often necessary where data are required on palatable and non-palatable browse groups (Rutherford 1979).

Another limitation is that mass predictions are only reliable within the range of CVols occurring in the sample (Telfer 1969), and it is particularly (even very slight) upward extrapolation in logarithmically transformed relations that may produce misleading data.

Despite the above limitations, CVol proved to be a useful measure of tree biomass, as indicated by the significant correlations obtained. Provided foliage densities are estimated consistently, the estimation of true LDM from a tree's CVol is possible. Although the allocation of foliage density scores is subjective, stronger correlations between CVol and LDM were obtained when compared with the correlation obtained without any correction for differences in foliage densities.

Conclusion

Our study provides a revised regression analysis method for estimating available browse biomass (measured by LDM) of savanna tree species from tree canopy volumes. By developing a reliable mathematical method of calculating CVol through the use of partial volumes, variation in canopy shapes, as well as differing feeding height restrictions of target large herbivores can be taken into account, increasing this method's usefulness in vegetation and large herbivore management and monitoring. Although individual study area models for each species have a higher prediction capacity, the general species models developed provide a means of applying these relations throughout properties in northern Zululand while still maintaining an acceptable level of accuracy, provided repeated measures are used and compared. The general models also provide a more objective means of determining the browsing capacity of a tree population, should the browse requirement of browsers be known, as well as the availability of browse during the year as influenced by the seasons. Since the calculation of LDM is dependent on the presence of leaves, for deciduous species, these calculated values will only be true should leaves remain on the tree during the winter period.

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CHAPTER 3. DETERMINANTS AND MEASUREMENT OF BROWSE PRODUCTION IN NORTHERN ZULULAND

“Without continual growth *and progress, such words as improvement,*
achievement, and success have no meaning.”
Benjamin Franklin

Abstract

In southern Africa, browse production data is in short supply. With the rapid expansion of wildlife ranching and conservation in South Africa and the resultant increase in the popularity of multi-species grazing and browsing systems, the browse production potential of a property is essential in determining its carrying capacity. The study aimed to reduce this knowledge gap by measuring browse production of seven key savanna tree species, common along the northern Zululand coast of KwaZulu-Natal, and to determine which biotic (measurable tree dimensions, tree species) and abiotic (climatic and soil) factors influence the rate and quantity of browse production of these species.

Regression trees are empirical models for understanding the response of continuous data to a set of explanatory variables. A regression tree model for browse production was developed from quarterly shoot growth increments measured over a 24-month period. Dominant factors influencing browse production, identified by the regression tree model, were available canopy volume (ACVol) (m^3), sampling season, species and height to the lowest leaves of the tree canopy (HL) (m).

Quarterly (3-month) browse production was greater on trees with larger available canopy volumes (up to a threshold) and with canopies that began closer the ground. Available canopy volume proved to be the most reliable predictor of browse production per species and per tree.

Browse production differed between sampling Periods, with a distinct growing season being identified. Growing season onset occurred during the sampling Period prior to the rainy season. Rainfall, particularly that fallen during the previous year, appeared to determine growing season length but not initiation of growth.

Tree species was identified as an important contributing factor to differences in browse production rates, suggesting the need for the development of species or species groups' models, rather than area-specific models on a more general scale. Browse production (kg/ha/quarter) was greatest in evergreen *E. divinorum,* followed by the semi-deciduous species, *S. africana* and *Z. mucronata*.

Introduction

The term savanna is widely accepted as describing vegetation with a herbaceous layer, dominated by grasses, with an upper layer of woody plants, which can vary from widely spaced to a 75% canopy cover, occurring in a seasonal summer rainfall environment (Rutherford and Westfall 1994). Trees and shrubs are by this definition critical components of savanna ecosystems providing a key resource for large herbivores, especially during the dry season (Cumming 1982, Bergström 1992). With the rapid expansion of the game ranching industry in South Africa, multi-species grazing and browsing systems have become increasingly popular, necessitating that we review the importance of browse in wildlife conservation and its role in carrying capacity determinations.

Of basic importance in the management of vegetation, and the animals themselves, is a knowledge of the diet of grazing and browsing animals combined with knowledge of the composition of the vegetation available to them (Barnes 1976). The feeding niches of African ungulates have often been classified in terms of three principal properties of the vegetation, namely its quality, quantity and botanical composition (Gordon and Illius 1996). The volume of vegetation available to an animal species at any time of the year, and the quality of this vegetation are possibly the most important determinants of a species' ecological carrying capacity.

Southern Africa has 23 species of large indigenous herbivores that weigh, on average, more than 100 kg and 22 that weigh less than 100 kg (Bothma et al. 2004). These herbivores can be divided into six main feeding types, namely obligate grazers with a diet of >90% grass, variable grazers with a diet of 60-90% grass, browser-grazer intermediates with a diet of 30-70% browse and grass and >20% wild fruits, generalists eating >20% of all food types, browsers with a diet of >70% browse and frugivores eating >70% wild fruits (Gagnon and Chew 2000). It is important to note that browse forms at least a small part of almost every large African herbivore's diet, with very few herbivore species being regarded as obligate grazers. Indeed, because the production of woody plant foliage is more predictable over time than that of grasses (Owen-Smith 1982), browse often forms a constant resource during winter, or in drought periods when grass is limiting. Any determinations of carrying capacity for a game ranching or wildlife conservation system, should therefore, take into account the browse component, more specifically the browse production potential, of the system.

In general, savanna browse biomass or production is little understood (Cissé 1980, Walker 1980, Pellew 1983a). Browse biomass is more difficult to measure accurately than biomass of herbaceous plants, as it is less uniformly distributed (Owen-Smith 1982) and there are no standardized techniques for its determination (Walker 1980, Pellew 1983a). Further, seasonal changes in available browse, dependent on the type of woody species, can be rapid and hence difficult to measure. Pellew (1983a) found that individual shoots of *Acacia* could grow up to 200 mm in a 48-hr period. This study has defined tree browse production to be the growth of new shoots (kg dry matter) over a given period of time (in this case 3 months or a year) ((Pellew 1981).

The rate of browse production has been linked to rainfall, tree species and ecological zone (Aucamp et al. 1978, Lamprey et al. 1980, Walker 1980, Pellew 1983a). In southern Africa, the few browse production figures that exist range from 1527 – 2240 kg/ha/annum (MAP c500 mm) (Dayton 1978, Goodman 1975). Studies in East Africa reported browse productivity rates reaching 5000 kg/ha/annum (MAP 800 mm) (Pellew 1981). Rutherford (1978), in Namibia, estimated the annual leaf production of *Burkea africana* Woodland savanna to be 1000 kg/ha/annum (MAP <550 mm). Finally, production figures for North Africa vary from 200 to nearly 1500 kg/ha/annum of edible browse (Le Houerou 1980). Studies of browse production are few and far between, with little standardization to allow direct comparisons. In South Africa, in particular, browse production (as defined by this study) has not yet been measured. Further, very little browse biomass data has been published for KwaZulu-Natal.

Our study aimed primarily at the measurement of browse production of seven key savanna tree species, common along the northern Zululand coast of KwaZulu-Natal. Furthermore, our study aimed to determine which biotic (measurable tree dimensions, tree species) and abiotic (climatic and soil) factors influence the rate and quantity of browse production of these species. More specifically we wished to explore the following unknowns: (a) to quantify seasonal browse production patterns, with the predication that browse production would be greatest during the wet season, (b) whether browse production differed among tree species; with the prediction that the relative browse production of deciduous species would be greater than that of evergreen species, and (c) whether browse production is related to tree size, in particular tree canopy size, with the prediction that browse production would be greater in larger trees with bigger, and more highly branched tree canopies. The investigation of the different biotic and abiotic factors affecting savanna browse production should increase our understanding of savanna browse dynamics and the resultant implications for herbivore carrying capacity.

Procedure

Study areas

Data were collected in the open wooded grassland areas of three game reserves in northeastern KwaZulu-Natal, Bonamanzi Game Park (BGP), Mun-Ya-Wana Private Game Reserve (MGR), and Pongola Game Reserve (North) (PGR). The three study areas are situated on an approximately north/south axis along the northern Zululand coastline and are situated along a distinct rainfall and temperature gradient (Figure 1.1). These differences allow for estimations of browse availability across a range of environmental conditions and provide an opportunity to observe the influence of such conditions on browse production.

Data collection

Selection of tree species

Attempts were not made to assess the productivity of whole woody communities because of the great diversity of species they contain. Instead, browse production was measured for seven key tree species, *Acacia nilotica*, *Carissa bispinosa*, *Dichrostachys cinerea*, *Euclea divinorum*, *Gymnosporia senegalensis*, *Spirostachys africana* and *Ziziphus mucronata*. These species represent a range of palatabilities, leaf sizes and tree guilds (Table 3.1). All seven species occurred at high densities across all three study areas.

Table 3.1: A comparison of the palatabilities, leaf sizes and tree guilds of the seven study tree species.

	A. nilotica	***C. bispinosa***	***D. cinerea***	***E. divinorum***	***G. senegalensis***	***S. africana***	***Z. mucronata***
Palatability	Favoured[3,4,5]	Favoured[2,4,5]	Favoured[4,7]	Not favoured[2,3,5]	Moderately favoured[5,6,9]	Highly favoured[4,5,6,8]	Highly favoured[1,4,5,6]
Ave Leaf size (mm)	4 x 1[4] (leaflet size)	40 x 20[4]	3 x 0.5[4] (leaflet size)	60 x 17[4]	70 x 50[4]	50 x 25[4]	60 x 35[4]
Leaf category*	Microphyllus	Mesophyllus	Microphyllus	Macrophyllus	Macrophyllus	Mesophyllus	Macrophyllus
Tree guild	Deciduous[4]	Evergreen[4]	Deciduous[4]	Evergreen[4]	Evergreen[4]	Semi-deciduous[4]	Semi-deciduous[4]

*Macrophyllus – having large or elongated leaves with usually many veins or a much branched vein (>60x20 mm)

*Mesophyllus – as for macrophyllous (<60x20 mm)

*Microphyllus – have small leaves with a single unbranched vein (<30x10mm)

1 (Bowland 1990)

2 (Owen-Smith 1979)

3 (Owen-Smith and Cooper 1987a)

4 (Pooley 1997)

5 (Rauff 2002)

6 (Sauer et al. 1977)

7 (Smits 1986)

8 (Tello and van Gelder 1975)

9 (Watson and Owen-Smith 2002)

Exclosure plots

To eliminate browsing, fenced exclosures were erected within the three study areas. The exclosures comprised 1.8 m high bonnox fencing, reinforced by iron standards of the same height. Fencing mesh size was graduated from top to bottom, with smaller mesh sizes at the bottom and larger sizes at the top. All browsing ungulates were effectively excluded from the trees within the exclosures. Individual trees, and not plots, were recognized as sample units, allowing plot size to vary according to the distribution of the tree species, the location of roads and the accessibility of browse. Plot sizes ranged between 100 and 450 m^2. Fencing was erected at least 3 m away from the nearest tree to the perimeter to eliminate the potential browsing by giraffe over the fence top. Plots were located in stands considered representative of the woody species community, with an adequate density and species diversity for production assessment, where there was evidence that extensive browsing had taken place on a number of tree species and where browsing animals were often observed to congregate (Table 3.2).

Table 3.2: Plot and species allocation across the study areas (Bonamanzi Game Park (BGP), Mun-Ya-Wana Private Game Reserve (MGR) and Pongola Game Reserve (PGR)).

	BGP	**MGR**	**PGR**	**Total**
Total plot size	1632 m^2	978 m^2	1730 m^2	**4339 m^2**
No. of plots	6	4	5	**15**
No. of individuals:				
A. nilotica	8	5	4	**17**
C. bispinosa	5	6	5	**16**
D. cinerea	0	4	3	**7**
E. divinorum	6	6	6	**18**
G. senegalensis	7	6	3	**16**
S. africana	4	6	5	**15**
Z. mucronata	0	6	4	**10**
Total	**30**	**39**	**30**	**99**

Browse production

Browse production was estimated using the method outlined by Pellew (1981), in which quarterly measurements of the length increments of unbrowsed tagged shoots of trees within the exclosures were used to determine production estimates. Thin, pliable wires, wrapped around the shoot were used as tags. The tags provided fixed base-line marks for the quarterly measurements. Tags were placed 15 cm back from the end of a shoot. Each tagged shoot was numbered with an aluminium label. Only shoots potentially accessible to browsing were tagged (i.e. occurring within 0.5 m of the edge of a tree canopy).

Shoot measurement was carried out across eight successive quarters (3 month seasons) beginning in July 2003 and ending in March 2005. At each measurement a standardized diagram of each tagged shoot was drawn from which any new growth (i.e. growth of the quarter immediately preceding the date of measurement) could be identified by comparison with the diagram of the previous measurement. Quarterly length increments (m/quarter) were thus determined for each shoot for seven sampling Periods (1 = Jul 03 – Sept 03; 2 = Oct 03 – Dec 03; 3 = Jan 04 – Mar 04; 4 = Apr 04 – Jun 04; 5 = Jul 04 – Sep 04; 6 = Oct 04 – Dec 04; 7 = Jan 05 – Mar 05).

Length increments were converted to weight increments (kg oven dry weight at 70^oC) by determination of length: weight conversion factors, after Pellew's method (1981). At each measurement, a sample of new growth shoots was clipped and weighed after being oven-dried. For each species, a mean conversion factor, specific to that quarter and canopy stratum (Figure 3.1), was calculated.

The subsequent stages in determining the rate of browse production are shown schematically in Figure 3.1. When estimating browse production on a per hectare basis, we recognised that, unlike the herbaceous stratum, trees tend to be heterogeneously distributed, often forming clumps of overlapping canopies (particularly along drainage lines) with large open areas with no trees between. From observation of the study sites, a density of 1000 trees/ha was chosen for this study, as it was representative of the open semi-arid savanna of the three study areas and gave each tree unit 10 m^2 of space, i.e. a square of ~ 3 x 3 m. The average tree canopy area in this study was 6 m^2.

The shoot density/m^3 of canopy volume was estimated by the use of a 0.5 x 0.5 m frame that was inserted at random into the canopy. The number of terminal shoots within the frame to a depth of 0.5 m (producing a frame volume of 0.125 m^3) was then counted. Twenty sample counts were taken to determine the mean shoot density m^3 of canopy of each stratum and of each species. Goodman (1975) used an open-ended cubic frame to estimate leaf density as a correction factor in his technique for determining total leaf biomass, while Pellew (1981) used such a frame to estimate shoot density in his technique for determining total shoot production of *Acacia* spp.

Canopy volumes (m^3) were calculated using the general volume equation (Equation 2.1) given in Chapter 2. Available CVol was defined as that portion of the tree canopy accessible to browsing by mammalian herbivores. For the purposes of this study, accessibility was restricted to a tree height of 5 m (the maximum browsing height of the tallest browser, giraffe (Pellew 1981)) and below, and a canopy depth of 0.5 m. Available canopy volumes (ACVol) (m^3) were therefore calculated by subtracting the volume of the outside 0.5-m perimeter of the canopy from the total canopy volume.

Collection of co-variate data

Within each plot, the following measurements were made on every tree: (i) maximum tree height (HT) (m), (ii) height to the lowest leaves of the canopy (HL) (m), (iii) average canopy diameter (D) (m), and (iv) stem diameter (Stem D) (m) at 0.5 m above ground. Each tree was assigned to a foliage density (FD) class (0-5) (defined in Chapter 2) at each quarter. Daily rainfall (mm), temperature maximums and minimums (^oC) and day length (hours) were collected for each study area (See Figure 1.2 and Figure 1.3). To investigate any influence of the soil nutrient status on browse production, three soil samples (top 15 cm) were taken from each plot in each study area and were analysed at Cedara Agricultural College for their physical and chemical properties. These included: clay concentration (%); phosphorus (P), potassium (K) and calcium (Ca) concentration (g/mL); pH; total cations ($cmol_c$/L) and organic carbon (%) (Table 1.2).

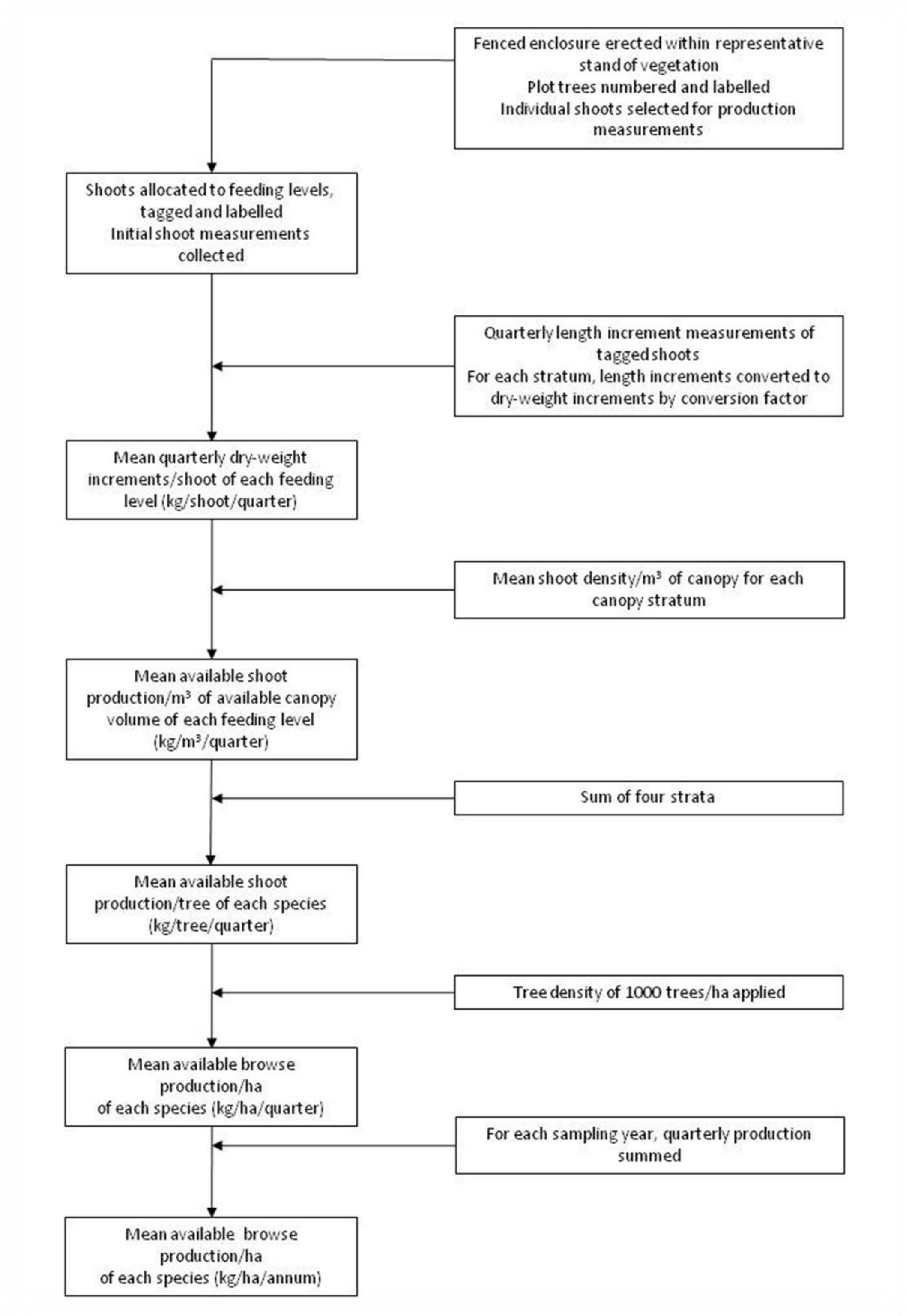

Figure 3.1: Stages in the determination of the mean browse production (kg/ha/quarter) after Pellew's (1981) method.

Data analysis

The choice of non-parametric models

Many ecological data sets tend to contain a large proportion of zero values (Martin et al. 2005). A data set may be termed 'zero inflated' when this number of zeros is so large that the data do not readily fit standard distributions (e.g. normal, Poisson, binomial, negative-binomial and beta) (Martin et al. 2005). Browse production data for this project yielded such a 'zero inflated' dataset (Figure 3.2). This was due to the fact that growth of many shoots across most of the tree species under observation was recorded as zero during at least one quarterly growing period. This was particularly true during the dormant or winter period, especially in the case of deciduous species. To overcome the distributional problems within the dataset, we used non-parametric approaches to model the factors influencing browse production.

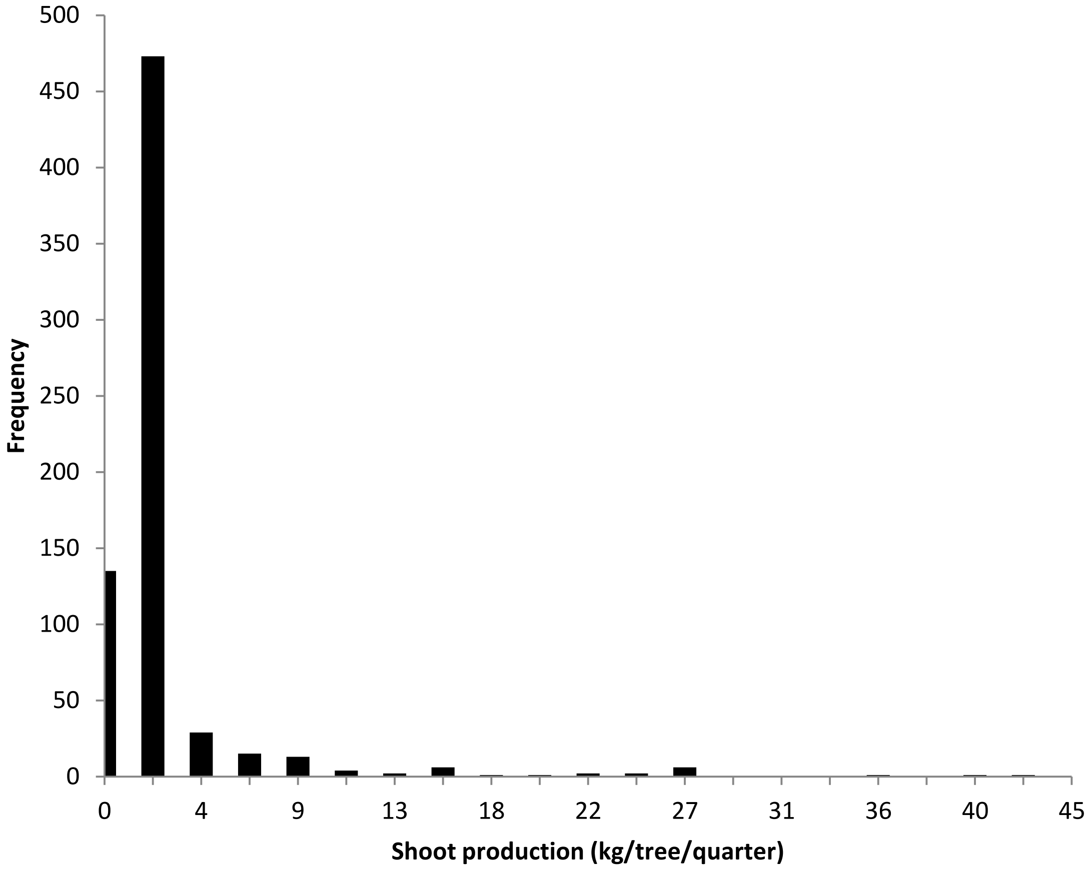

Figure 3.2: Histogram of browse production (kg/tree/quarter) (*n*=693) for the period July 2003 - March 2005.

Modelling using regression trees

Classification and regression trees (CART®) are binary decision trees accounting for the variation of a single response variable by one or more categorial or numerical explanatory variables respectively. Regression trees were constructed using CART5.0 (Steinberg and Colla 1997) for browse production (kg/ha/quarter) for the whole study area. Explanatory variables comprised binary codes for study area (BGP, MGR and PGR), seven tree species (*A. nilotica*, *C. bispinosa*, *D. cinerea*, *E. divinorum*, *G. senegalensis*, *S. africana*, *Z. mucronata*), sampling Period (1 = Jul-Sep 2003, 2 = Oct-Dec 2003, 3 = Jan-Mar 2004, 4 = Apr-Jun 2004, 5 = Jul-Sep 2004, 6 = Oct-Dec 2005, 7 = Jan-Mar 2005), foliage density (0-5), and numerical values for ACVol (m^3), HT (m), HL (m), Stem D (m), cumulative mean monthly rainfall for each quarter (MMR) (mm) and maximum and minimum mean daily temperatures (MMaxDT and MMinDT respectively) (^oC), soil clay conconcentration (%), P, K and Ca concentration (g/mL); pH, total cations ($cmol_c/L$) and organic carbon (%) in the soil.

CART® recursively partitions the multidimensional space defined by the predictor variables into zones that are as homogenous as possible in terms of the response (Vassières et al. 2000). Each dichotomy shows the explanatory variable which best divides the data into relatively homogenous groups. In contrast to most conventional modelling approaches, CART® seeks to reveal multiple structures in heterogeneous data by identifying the hierarchy of context dependent (i.e. interactive) effects of explanatory variables, such as rainfall and/ or tree height (Morris and Fynn 2003). CART® is an established method in medical diagnosis but has found applications in plant (Morris and Fynn 2003, Vassières et al. 2000) and wildlife ecology (De'Ath and Fabricus 2000).

Differences in browse production (kg/ha/quarter) among the different key influencing factors identified by CART® were determined with repeated measures analysis of variance (ANOVA) (Genstat 9.1.0.147, Lawes Agricultural 2006). With repeated measurements, there is likely to be a greater correlation between observations that are made at adjacent time points than between those that are more greatly spaced (Payne et al. 2006). To correct for this correlation, a correction factor (epsilon), as described by Greenhouse and Geisser (1959), was applied.

Results

Regression tree model

The regression tree model is illustrated for browse production (kg/ha/quarter) across the entire study area (Figure 3.3). Browse production was primarily, influenced by tree ACVol (m^3) (with 7 % of the total variance for the model being accounted for). Other important factors affecting quarterly browse production were: sampling Period (1 %), height to lowest leaves (m) (12 %), species (2 %) and potassium (mg/L) (0.2 %), with the total model accounting for 32.5 % of the total variance in the dataset.

Browse production was greatest during a distinct growing season (sampling Periods 2 and 6) in larger trees with bigger ACVols (>12.32 m^3), with canopies lower to the ground level (<0.08 m), and in highly branched evergreen and semi-deciduous trees (particularly *E. divinorum* (4) and *C. bispinosa* (2), and to a lesser extent, *S. africana* (6) and *Z. mucronata* (7)). Higher levels of soil potassium (>143 mg/L) were associated with double the browse production from 690 kg/ha/quarter (n = 127) to 1300 kg/ha/quarter in the sampling Periods 1,3,4,5 and 7.

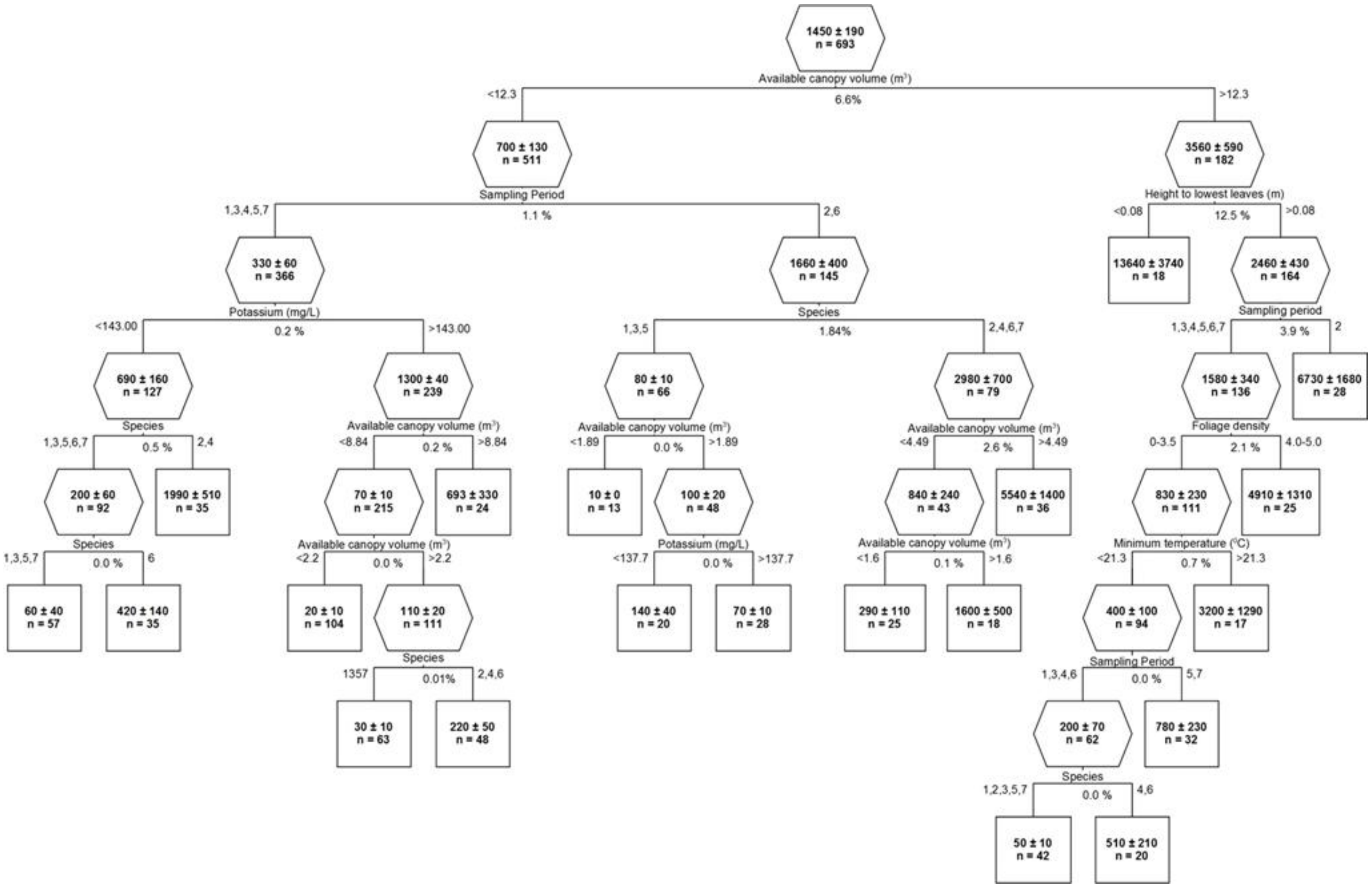

Figure 3.3: Regression tree for the browse production (kg/ha/quarter) of *A. nilotica* (1), *C. bispinosa* (2), *D. cinerea* (3), *E. divinorum* (4), *G. senegalensis* (5), *S. africana* (6) and *Z. mucronata* (7) across three study areas (BGP, MGR, PGR) and seven sampling Periods (Jul-Sep 2003 (1), Oct-Dec 2003 (2), Jan-Mar 2004 (3), Apr-Jun 2004 (4), Jul-Sep 2004 (5), Oct-Dec 2004 (6), Jan-Mar 2005 (7)), subject to various combinations of tree physical dimensions, soil nutrients, climatic variables and tree canopy foliage density (see *Data collection*). Means (±SE) for each group are presented at each dichotomy together with the splitting criterion and the percentage of the total variance accounted for by that division. Means (±SE) and the number of members of each group in the terminal (rectangle) and non-terminal (broken rectangle) leaf node are presented. Browse production values are based on a tree density of 1000 trees/ha.

Major factors influencing browse production

Available Canopy volume (m^3)

Mean quarterly browse production (kg/ha/quarter) for ACVols less than 12.3 m^3 (700 ± 130 kg/ha, *n* = 511) was considerably less than that for larger ACVols in excess of 12.3 m^3 (3560 ± 590 kg/ha/quarter, *n* = 182) (Figure 3.3). Mean quarterly browse production differed between ACVol groups ($F_{5,687}$ = 11.718, $P<0.001$) (Figure 3.4), increasing from 219 kg/ha/quarter (0-3 m^3) to a maximum of 5507 kg/ha/quarter (30.1-40 m^3) before leveling off.

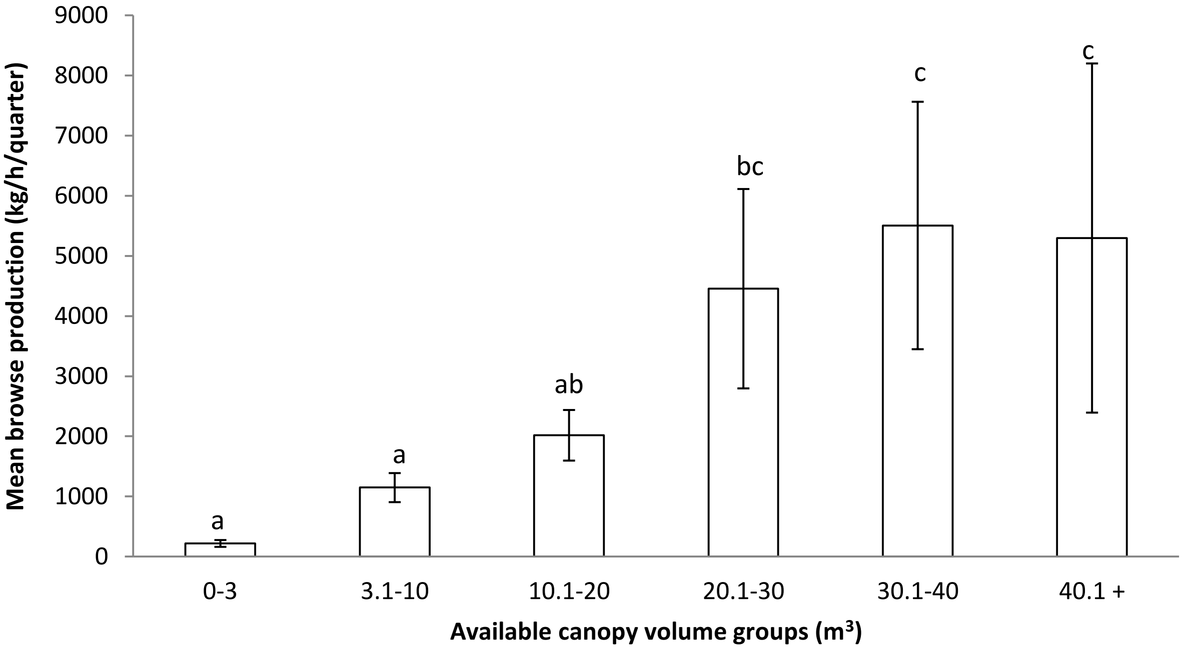

Figure 3.4: Mean browse production for different available canopy volume groups with SE. Letters above the bars indicate significant differences ($P<0.05$) between the available canopy volume groups (m^3). Browse production values are based on a tree density of 1000 trees/ha.

Height to lowest leaves (m)

In trees with larger ACVols (>12.3 m^3) (Figure 3.3), HL (m) was the most important influencing factor of browse production with a relative variable importance of 70 %. Trees with large canopy volumes and HLs <0.08 m from the ground recorded production five times greater (13640 ± 3740 kg/ha/quarter, *n* = 18) than trees whose canopies started higher off the ground (2460 ± 430 kg/ha/quarter, *n* = 164). Mean browse production differed between HL groups

($F_{3,689}$ = 9.454, $P<0.001$) (Figure 3.5), decreasing from 3597 kg/ha/quarter (0-0.05 m) to a minimum of 879 kg/ha/quarter (0.51-1.50 m).

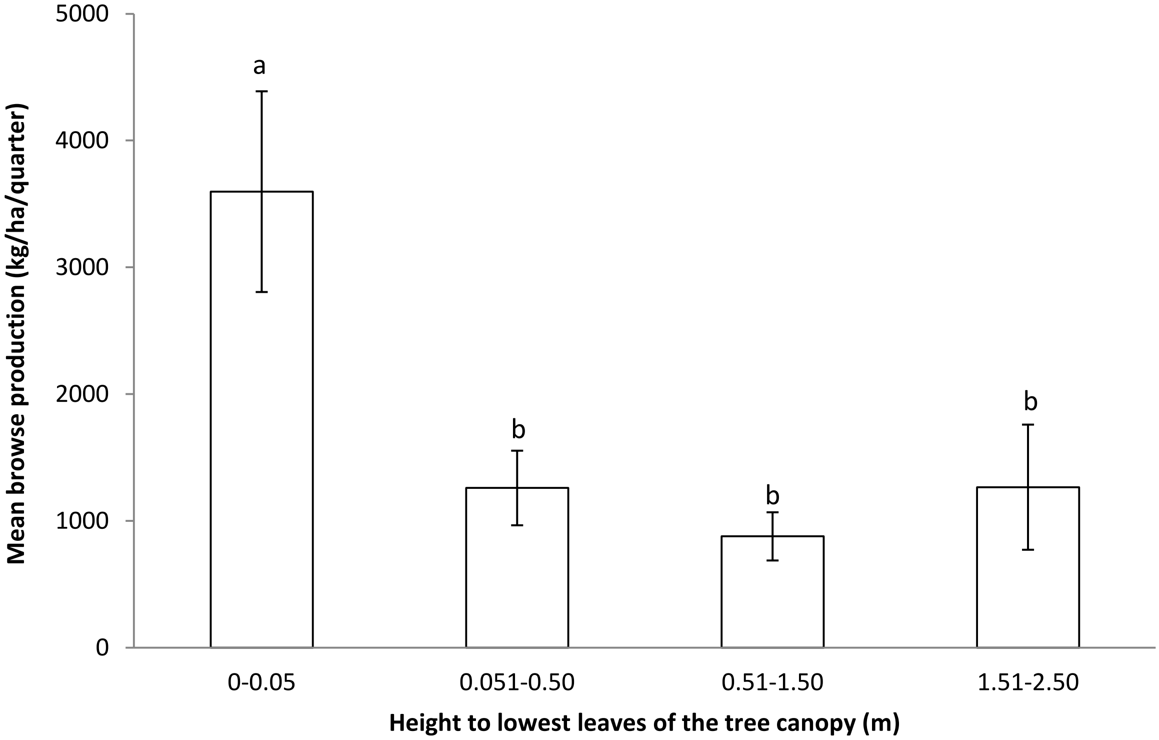

Figure 3.5: Mean browse production for different height to the lowest leaves of the tree canopy groups with SE. Letters above the bars indicate significant differences ($P<0.05$) between the height groups (m). Browse production values are based on a tree density of 1000 trees/ha.

Sampling Period

The browse production of trees with smaller available canopy volumes (<12.3 m^3) was primarily affected by sampling Period with a relative variable importance of 25 % (Figure 3.3). A heightened mean browse production of 1660 ± 400 kg/ha/quarter (*n* = 145) occurred during sampling Periods 2 and 6 (Oct-Dec 2003 and Oct-Dec 2004 respectively) compared with 330 ± 160 kg/ha/quarter (*n* = 127) during the other seasons. Sampling Period was also a secondary factor (accounting for 4 % for the variability) influencing the browse production of larger trees with browse production being 4.25 times greater in sampling Period 2 (6730 ± 1680 kg/ha/quarter, *n* = 28) than for any of the other Periods (1580 ± 340 kg/ha/quarter, *n* = 136).

Mean browse production differed between sampling Periods ($F_{6,686}$ = 6.567, $P<0.001$) (Figure 3.6), with sampling Periods 2, 5 and 6 recording the greatest browse production. Frost (1985) reported that tree growth is not dependent on current rainfall as growth is initiated before the rains come. Comparing mean quarterly rainfall (mm) with mean browse production confirms this observation for our study (Figure 3.6). Heightened rainfall is experienced during sampling Periods 3 and 6 while the start of each growing season occurs in the previous quarter.

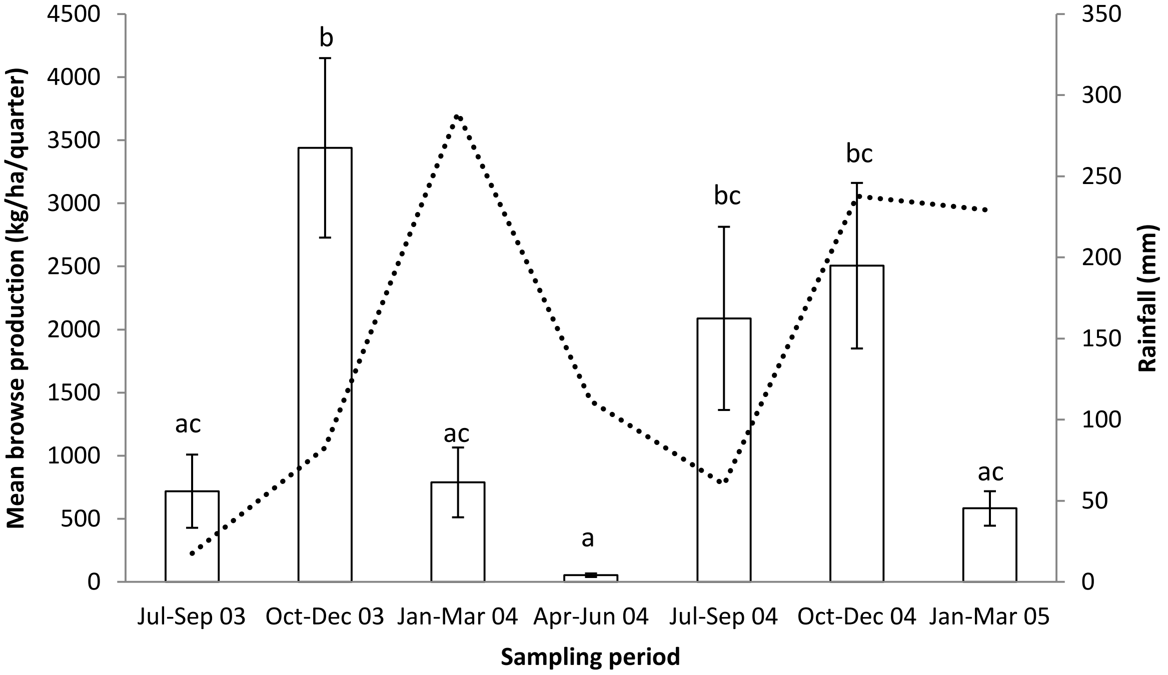

Figure 3.6: Mean browse production (kg/ha/quarter) and rainfall (mm) for each sampling Period with SE. Letters above the bars indicate differences (*P*<0.05) between sampling Periods. Browse production values are based on a tree density of 1000 trees/ha.

Table 3.3: Annual rain fallen during the study at each study area (Bonamanzi Game Park (BGP), Mun-Ya-Wana Private Game Reserve (MGR) and Pongola Game Reserve (PGR)) with mean (measured over 20 years) annual rainfall (MAR) for each site.

	BGP	MGR	PGR
MAR	807.8	606.7	523.3
2002	549.6	267.7	275.0
2003	786.5	323.1	190.8
2004	1021.6	595.7	310.3
2005	873.4	476.2	271.0

Species

Mean browse production was 37 times greater in *C. bispinosa* (2), *E. divinorum* (4), *S. africana* (6) and *Z. mucronata* (7) (2980 ± 700 kg/ha/quarter, *n* = 79), during sampling Periods 2 and 6, in trees with a ACVol < 12.3 m^3 compared to

A. nilotica (1), *D. cinerea* (3) and *G. senegalensis* (5) (80 ± 10 kg/ha/quarter, *n* = 66) (Figure 3.3, Table 3.4). During the remaining sampling Periods, only *C. bispinosa* and *E. divinorum* (1990 ± 510 kg/ha/quarter, *n* = 35) showed higher mean production in trees with a canopy volume < 12.32 m^3 compared with *A. nilotica, D. cinerea, G. senegalensis, S. africana* and *Z. mucronata* (200 ± 60 kg/ha/quarter, *n* = 92). In trees with larger ACVols, *E. divinorum* and *S. africana* (510 ± 210 kg/ha/quarter, *n* = 20) showed greater production rates during the sampling Periods 1,3,4,5,6 and 7 compared with the other species (50 ± 10 kg/ha/quarter, *n* = 42).

Mean browse production differed among tree species ($F_{6,686}$ = 6.966, *P*<0.001), with *E. divinorum* having the greatest production and *D. cinerea* the least (Figure 3.7).

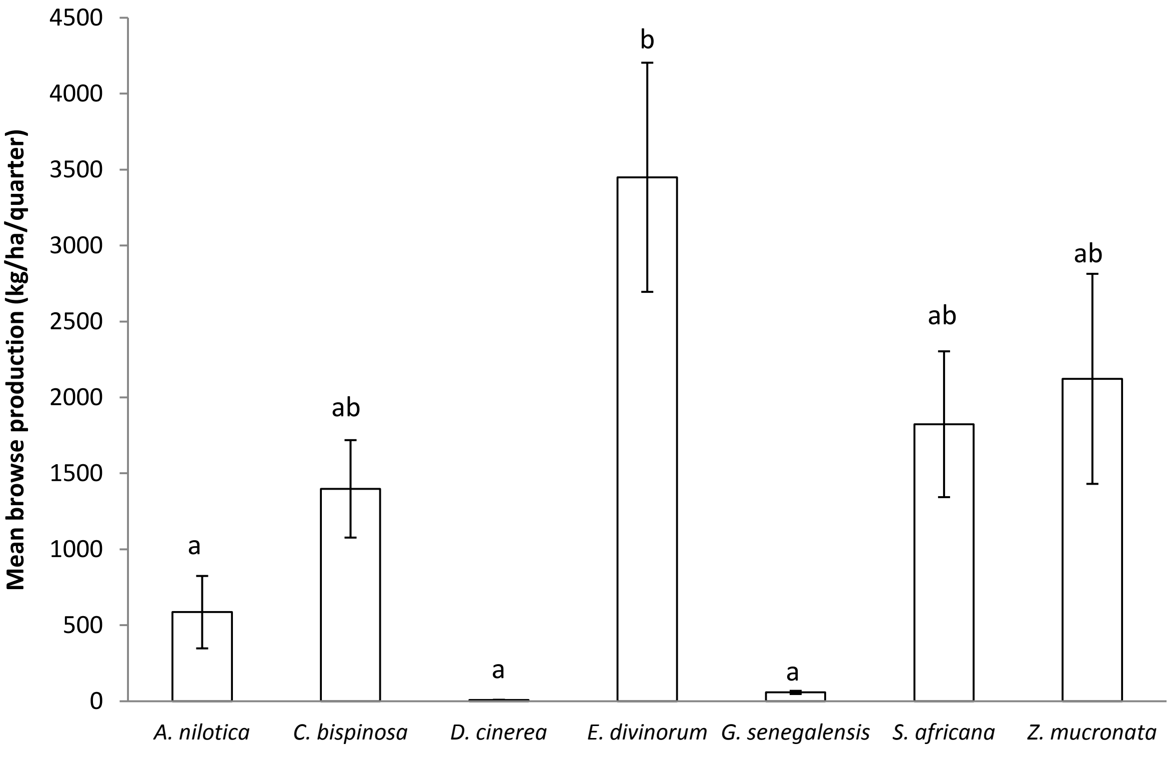

Figure 3.7: Mean browse production for each species with SE. Letters above the bars indicate significant differences (*P*<0.05) between species. Browse production values are based on a tree density of 1000 trees/ha.

E. divinorum consistently had the greatest browse production, across both study years and all sampling Periods, while *D. cinerea* consistently produced the least amount of browse (Table 3.4). All species, with the exception of *S. africana* and *Z. mucronata*, showed greater browse production in the second study year following the improved rainfall (Figure 1.2). While browse production in sampling Periods 1,3,4 and 7 was considerably less than that during sampling Periods 2, 5 and 6 (the growing season), it is noteworthy that browse production occurred year round.

Table 3.4: Mean annual, growing season (sampling Periods 2, 5, 6) and non-growing season (sampling Periods 1, 3, 4, 7) browse production for each species, measured over two years along the northern Zululand coast of KwaZulu-Natal. Browse production values are based on a tree density of 1000 trees/ha.

Tree Species	**Mean annual production (kg/ha/annum ± SE)**		**Mean growing season production (kg/ha/quarter ± SE)**		**Mean non-growing season production (kg/ha/quarter ± SE)**	
	Year 1	**Year 2**	**Year 1**	**Year 2**	**Year 1**	**Year 2**
Acacia. nilotica	1760 ± 1347	2346± 1366	1973 ± 1319	1260 ± 670	78 ± 32	164 ± 86
Carissa bispinosa	4935 ± 1882	4893± 2338	1981 ± 721	1898 ± 1134	4 ± 1	362 ± 211
Dichrostachys cinerea	20 ± 10	28 ± 11	12 ± 7	14 ± 6	4 ± 4	0 ± 0
Euclea divinorum	10720 ± 3306	13588± 5349	5153 ± 2427	5405 ± 2792	2175 ± 1371	723 ± 309
Gymnosporia. senegalensis	192 ± 35	221 ± 77	63 ± 24	85 ± 40	6 ± 2	19 ± 6
Spirostachys africana	7587 ± 2696	5258 ± 1935	6254 ± 2611	3790 ± 1491	491 ± 163	489 ± 218
Ziziphus mucronata	7628 ± 1824	7250 ± 4012	7327 ± 1470	6342 ± 4123	862 ± 361	302 ± 193

Discussion

While the regression tree model presented indicates that the effect of species on browse production was not as important as ACVol as a predictor, the wide range (20 (*D. cinerea)* – 12229 (*E. divinorum*) kg/ha/quarter) of browse production for the different species in this study is both substantially less and substantially greater than had been previously recorded for savanna browse (Table 1.1). Browse productivity has been closely related to species, rainfall and ecological zone (Otsyina and McKell 1985). In fact, Walker (1980), in his review of browse and its role in livestock nutrition, goes as far as to say each tree species needs to be examined separately due to the high variability in production data among species. With this in mind, the development of species or species group production models needs to be undertaken in order to improve the prediction accuracy of the browse production (Chapter 4).

The annual browse production values for *C. bispinosa, E. divinorum, S. africana* and *Z. mucronata* in this study are of the order of above-ground production values reported for east African savanna grasslands. Sinclair (1975) estimated grass production in the Serengeti short grasslands to be about 4000 kg/ha and 2500 kg/ha for the long grasslands during one growing season of about 8 months at 500 mm rainfall. Annual browse production can therefore, in some habitats, match or even exceed grass production.

Browse production related to tree canopy size

The available browse biomass of a tree is highly correlated with various physical dimensions of the plant, particularly canopy volume (Kelly and Walker 1976, Smit et al. 1996, Smit 1996). It is thus plausible that the production potential of any individual tree will also be influenced by its current ACVol.

The number, size and arrangement of branches making up a tree canopy determine the volume of that canopy. If this is true, one might infer that the greater the canopy volume, the greater the number of branches making up that canopy, in three dimensions. Since trees restrict all growth to branch tips, due to apical dominance (in the absence of browsing), it is intuitive that ACVol would be a good predictor of browse production. Cissé (1980) established a relation between crown area and tree production in *Acacia albida*, *Acacia seyal*, *Pterocarpus lucens* and *Ziziphus mucronata*. In this study, tree species with larger ACVols that were highly branched with multiple growing tips, like *C. bispinosa* and *E. divinorum*, for example recorded higher browse production. It is noted that canopy volume is related to tree growth, and that the greater levels of growth may result in larger trees with larger canopies. Available canopy volume, however, serves as a useful predictor of seasonal browse production.

Browse production reached a plateau at increasing canopy sizes. Within a single tree, branches growing in more favourable conditions (i.e. those at the outer canopy) are allocated more limiting resources at the expense of other branches (Henriksson 2001). Further, young branches tend to grow vigorously, although they are usually small in size, while old branches are often large but slower to grow (Novoplansky 2003). The same relation may also exist for younger, smaller trees versus older larger trees, where growth is seen to be more vigorous in younger, smaller trees and less vigorous in older, larger trees. While the absolute production rates of large trees (as a function of their greater number of shoot bearing branches) remains greater than that of smaller trees, their relative growth rates may be lower. Since most of the canopy of smaller trees can be considered ‘available’ to mammalian browsing herbivores, this relation is important, in terms of game management and carrying capacity determinations and merits further study.

Our regression tree model indicated that in trees with larger ACVols, HL was the most important influencing factor of browse production. While we have established above that canopy measures are useful determinants of browse production for the season measured, large trees with HLs <0.08 m from the ground recorded greater production. This result does not infer a production advantage in bigger trees that have canopies that start lower to the ground, but rather can be attributed entirely to the growth habit and production capacity of *E. divinorum.* All of the individual trees with large tree ACVols (>12.3m^3) and HLs <0.08 m from the ground were *Euclea* spp*.* *Euclea divinorum* are often multi-stemmed, much branched trees with rounded canopies that often ‘sweep’ ground level (Pooley 1997). In this study, *E. divinorum* had the greatest browse production, across both study years and all sampling Periods. It is also noted that browse production remained high in *E. divinorum* trees with tree canopies higher off the ground.

Influence of season on browse production

The fact that browse production is influenced by sampling period (inferred season), is an important result in terms of the management and conservation of browse. Browse production during the growing season essentially determines the amount of browse available to mammalian herbivores in the year ahead, as well as the tree's ability to respond to the defoliation (or any other stress for that matter) of the previous season. Comparing the browse production figures during the growing season of consecutive years would supply land managers with valuable insight into whether the browse component of the system is under stress, is maintaining, or perhaps is encroaching.

In our study, a distinct growing season (sampling Periods 2: Oct 03 – Dec 03, 5: Jul 04 – Sep 04, 6: Oct 04 – Dec 04) was observed, despite browse production occurring year round, on average, in all of the tree species studied. The start of the growing season for both study years began in the sampling Period prior to the start of the rainy season. Several studies have indicated that the start of the growing season appears to be related more to changes in temperature than to rainfall (Rutherford and Panagos 1982, Milton 1987), although daylength has also been identified as a possible factor (Milton 1987). Because savanna trees commonly initiate leaf flush prior to the start of the rainy season (Milton 1987, Zietsman et al. 1989) it is plausible that rainfall is not the proximate trigger. While rainfall may not trigger leaf and shoot flush in savanna trees, it influences annual production (greater production in greater rainfall areas) (Shackleton 1999) as well as the duration of the growing season (increasing aridity concentrating phenological activity into a shorter period) (Shackleton 1999, Hoffmann 1989 cited by). Further, Scholes and Walker (1993) suggested that growing season length is influenced by the carry-over of soil moisture, which is likely to be lower at more arid sites. Interestingly, during the first sampling year, the growing season was confined to a single quarter (Oct-Dec 2003), while in the second year; the growing season extended over two quarters (Jul-Dec 2004). Scholes and Walker (1993) suggested that growing season length is influenced by the amount of rainfall, carried over from the previous season (in terms of soil moisture availability). In 2002, the year prior to the commencement of the study, below average rainfall fell across all of the study areas (Table 3.3). Subsequent years showed a steady increase in rainfall, with above average rainfall falling on BGP in 2004. The fact that browse production did occur year round is also important because at the end of the growing season when grass production ends and herbaceous forage is scare, some tree species are still actively producing browse. The significance of this production at the most nutrient-limited time of year is an important consideration in any carrying capacity determination.

The length of the growing season has a marked effect on the production potential of savanna tree species. In determining the browsing capacity of an area, therefore, the length of the growing season will have a profound effect on the capacity of the area to sustain more browsers. In terms of modelling or predicting browse production, the amount of rainfall carried over from the previous season (in terms of soil moisture availability) has an even greater effect on browse production and the length of the growing season. Sustained periods of drought or high rainfall will produce large differences in predicted browse production values, with the suggestion that browse production is likely to decrease at a steady rate for each consecutive year of below average rainfall. The important implication is that managers have a timely predictor of carrying capacity that they can use to adjust stocking rate depending on the previous rainfall.

Browse production differences among tree species

Our study was aimed largely at investigating factors affecting browse production in African savannas. The accurate prediction of browse production is of value to any management system, whether conservation, game ranching or even game farming, as it allows for some degree of monitoring to take place and for estimates of game carrying capacities to be determined. A plant’s ability to recover from a loss of new shoots differs among species as well as the intensity and frequency of defoliation. This is an important management concern, especially because mammalian browsers, being highly selective feeders, show marked preference for certain key species, tending to leave almost untouched less ‘palatable’ species (Owen-Smith and Cooper 1983, 1987a, Owen-Smith 1979, Owen-Smith and Cooper 1985, Dziba et al. 2002, Scogings et al. 2004, Dziba et al. 1999). With this in mind, the further investigation of factors affecting browse production, at a species level, is given in Chapter 4, with the aim of improving the prediction capacity of the browse production management models developed.

Conclusion

Our study has reduced the knowledge gap regarding the measurement and prediction of browse production in South Africa, specifically in KwaZulu-Natal. Browse production was shown to differ among sampling Periods, with a distinct growing season identified. Furthermore, the onset of the growing season occurred during the sampling Period prior to the rainy season and rainfall, particularly that fallen during the previous year, was seen to be more closely linked with the length of the growing season rather than its initiation. Browse production varied among tree species with evergreen *E. divinorum* having the greatest mean browse production (kg/ha/quarter) followed by the semi-deciduous species, *S. africana* and *Z. mucronata*. Annual browse production figures (kg/ha/annum) for all species, except *D. cinerea* and *G. senegalensis*, are greater than any recorded browse production estimates for southern Africa. Lastly, the use of ACVol as a seasonal measure of browse production (for annual comparison purposes) is supported.

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CHAPTER 4. BROWSE PRODUCTION COMPARISONS BETWEEN EVERGREEN, SEMI-DECIDUOUS AND DECIDUOUS SAVANNA TREE SPECIES OF NORTHERN ZULULAND

"Every species of plant is a law unto itself."
Henry A. Gleason

Abstract

South African savannas are poorly studied with respect to canopy growth and browse production, making it difficult to quantify the available browse biomass on which browsing capacity estimations are based. Our study addressed these issues by comparing the browse production of evergreen (*Carissa bispinosa, Euclea divinorum, Gymnosporia senegalensis*), semi-deciduous (*Spirostachys africana, Ziziphus mucronata*) and deciduous (*Acacia nilotica, Dichrostachys cinerea*) savanna tree guilds along the northern Zululand coastline of KwaZulu-Natal. Differences in annual (at various levels in the tree canopy as well as with and without defoliation), growing/non-growing season and wet/dry season production were investigated.

Results showed that mean annual browse production of semi-deciduous tree species was greater than that of deciduous and evergreen species. Mean quarterly browse production was greatest, for all tree species, during the growing season, with the greatest difference between growing and non-growing season production being observed in deciduous forms. Evergreen forms showed continuous growth over the entire study, with a period of enhanced growth over the wet season. Deciduous forms, on the other hand, concentrated growth in spurts, when environmental conditions became favourable, with most production occurring during a short growing season.

Distinct differences in browse production were observed at different feeding heights in the canopy for all tree guilds. Mean annual browse production followed the trend: 0.0-0.5 m>0.5-1.5 m>1.5-2.5 m>2.5-5.0 m, in the absence of browsing herbivores.

Moderate defoliation resulted in increased short-term levels of browse production in all three tree guilds, when compared with the control. The effect of defoliation on browse production was greater during the growing season, than in any other season, and had a lasting effect over the rest of the year.

Differences in the production and available browse biomass among the different tree guilds and seasons have a profound effect on the determination of browser carrying capacities and need to be incorporated into any game or conservation management plan.

Introduction

Sub-tropical deciduous and evergreen trees frequently occupy different habitat types (Antúnez et al. 2001). Several hypotheses have been proposed for the advantages of having a deciduous or evergreen habit (Chabot and Hicks 1982, Antúnez et al. 2001, Singh and Kushwaha 2005), including drought and freezing avoidance, resource conservation (carbohydrates and/or nutrients), control of nutrient recycling and time to recoup the cost of leaf construction. Trees in semi-arid southern African savannas must survive the sometimes long dry season by either avoiding (deciduous) or tolerating (evergreen) dry periods (Singh and Kushwaha 2005). The co-occurrence of evergreen and deciduous species in African semi-arid savannas, however, suggests rather that deciduous and evergreen species employ different strategies to deal with the same conditions (Givnish 2002). It is the difference in these strategies, on a general level, that have a profound effect on the rate, quantity and seasonality of browse production and therefore the management of browse resources for browsing ungulates.

Plant browse production is one of the more important components of vegetation with respect to browse availability in some ecosystems and nutrient cycling, especially in deciduous plant ecosystems (Rutherford and Panagos 1982). The concepts of browse, available browse, browse utilisation and browse production were discussed at length in Chapter 2 and Chapter 3. When leaves are present, deciduous tree species tend to have greater relative growth rates, specific leaf areas (SLAs) and relative photosynthetic efficiency than evergreen tree species growing under similar conditions (Reich et al. 1992, Antúnez et al. 2001, Choat et al. 2005, Singh and Kushwaha 2005, Givnish 2002). The greater relative growth rate (RGR) of deciduous species is thought to give them a greater competitive ability and is seen as an important determinant of their spatial distribution (Cornelissen et al. 1996, Cornelissen et al. 1998). Because of food preferences, browse being available does not necessarily mean that it will be eaten. Browsers select among plant species as markedly as grazers do, if not more so (Grunow 1980).

The aim of our study was to measure the browse production of key evergreen, semi-deciduous and deciduous savanna tree species, common along the northern Zululand Coast of KwaZulu-Natal, representing a range of published palatabilities to ungulates and leaf sizes. More specifically we wished to determine whether: (a) the rate and quantity of browse production between evergreen and deciduous species was similar, with the prediction that the rate of browse production during the growing season would be greater in deciduous species; (b) browse production within a species guild differed between growing and non-growing seasons, with the prediction that growing season browse production would be greater than non-growing season production; (c) the production of browse at different levels in the canopy was different, with the prediction that browse production would be greater at higher levels in the tree canopy; and lastly (d) the removal of leaf and shoot material induces a production response of the tree, with the prediction that leaf and shoot removal would have a positive effect on browse production. The investigation of these questions should further increase our understanding of savanna browse production dynamics by taking into account differences among the browse production of the deciduous, semi-deciduous and evergreen woody species guilds. Such knowledge would be useful for improving modelling of browse production (Chapter 6) in seasonal, semi-arid zones in southern Africa, with the aim of improving browsing herbivore carrying capacity estimates.

Procedure

Study areas

Data were collected on three game reserves situated on an approximately north/ south axis along the northern Zululand coastline of KwaZulu-Natal. The study areas from north to south, following a rainfall gradient from dry to wet (Figure 1.1, Figure 1.2), were Pongola Game Reserve (PGR), Mun-Ya-Wana Private Game Reserve (MGR) and Bonamanzi Game Park (BGP). Data collection occurred on open wooded grassland areas within the Lowveld Bioresource group, as described by Camp (1997). The differences in rainfall, temperature and soil properties between the study areas (Chapter 1, Study areas) allow for estimations of browse availability across a range of environmental conditions and provide an opportunity to observe the influence of such conditions on browse production.

Data collection

Browse production was measured for seven key tree species, representing three guilds: deciduous (*Acacia nilotica* and *Dichrostachys cinerea*); semi-deciduous (*Spirostachys africana* and *Ziziphus mucronata)*; and evergreen (*Carissa bispinosa, Euclea divinorum* and *Gymnosporia senegalensis*), across eight seasons and seven sampling Periods (1 = Jul 03 – Sept 03; 2 = Oct 03 – Dec 03; 3 = Jan 04 – Mar 04; 4 = Apr 04 – Jun 04; 5 = Jul 04 – Sep 04; 6 = Oct 04 – Dec 04; 7 = Jan 05 – Mar 05) for stratified browsed and unbrowsed trees. These species were chosen because they represent a range of palatability to ungulates and leaf sizes (Table 3.1), were common, and occurred at high densities across all three study areas.

Defining growing/non-growing and wet/dry seasons

Chapter 3 recognized a distinct growing season for both sampling Year 1 (sampling Period 2: Oct-Dec 2003) and sampling Year 2 (sampling Periods 5: Jul-Sep 2004 and 6: Oct-Dec 2004). Despite browse production being recorded in the rest of the sampling Periods, for means of comparison periods 1(Jul-Sep 2003), 3 (Jan-Mar 2004), 4 (Apr-Jun 2004) and 7 (Jan-Mar 2005) are grouped together and collectively termed the ‘non-growing’ seasons.

For the purposes of our study, the wet season is defined as the period during the year when most of the annual rainfall in the region falls (more than 80% of the annual precipitation) (Table 4.1). Conversely, the dry season, is defined as the period of the year during which precipitation is at a minimum for the region (i.e. below 20% of the annual rainfall) (Table 4.1). A distinction is made in this study between growing season (sampling Periods 2, 5 and 6) and wet season (sampling Periods 3, 6 and 7) as periods of increased production (i.e. growing season) were recorded in sampling Periods prior to the onset of the wet season. Savanna trees are known to initiate growth prior to the onset of the rainy season (Murali and Sukumar 1993, Higgins et al. 2011, Teague and Walker 1988b) and the distinction in our study between growing and wet seasons recognises this.

Table 4.1: Division of sampling Periods into wet and dry seasons based on mean quarterly rainfall for the whole study area.

Year	Quarter	Mean Rainfall (mm/quarter)	Percentage of annual rainfall	Season
2003	Jul-Sep	32.7	6.3	dry
2003	Oct-Dec	80.5	15.6	dry
2004	Jan-Mar	273.6	44.4	wet
2004	Apr-Jun	41.0	6.7	dry
2004	Jul-Sep	92.7	15.0	dry
2004	Oct-Dec	209.2	33.9	wet
2005	Jan-Mar	312.3	51.8	wet

Stratification of the tree canopy and sampling Periods

Because of the extreme variability of individual shoot increments and shoot densities within tree canopies (Pellew 1983a), it was evident before measurements began that browse production estimates would produce very large standard errors. To try to reduce these variances, the canopies of the trees within the exclosures were stratified. Stratification of the tree canopy into height classes (Telfer 1969) or classification of whole canopies into foliage density classes (Mason and Hutchings 1967) reduces the variances of browse production estimates.

This stratification was also partly influenced by the fact that, in vegetation where much leaf occurs above the reach of browsing animals, it is necessary to define the height to which animals can browse and to relate dimensions to the yield of edible material below this level (Barnes 1976). A range of browsing ungulates was observed within the study area, all feeding at different levels. These included, giraffe (1-5m), impala (0-1.5m), nyala (0-1.5m), kudu (0-2.1m), red duiker (0-0.5m), common duiker (0-0.5m), and bushbuck (0-1.75m) (du Toit 1990, Woolnough and du Toit 2001, Makhabu 2005) (Table 1.3). Four feeding levels were recognised to allow for accurate determination of the browse production (kg/ha) available for the different ungulates within the study areas. These feeding levels were: 0 – 0.5 m; 0.5 – 1.5 m; 1.5 – 2.5 m; and 2.5 – 5 m. On any one tree within the exclosure plots, shoots were tagged within all browsing levels on that tree (Table 4.2).

Table 4.2: Division of tagged shoots across species and feeding level.

Species	Feeding Level				Total
	0.0 – 0.5 m	0.5 – 1.5 m	1.5 – 2.5 m	2.5 – 5.0 m	
A. nilotica	2	23	41	31	97
C. bispinosa	20	32	15	0	67
D. cinerea	0	15	9	8	32
E. divinorum	10	37	43	20	110
G. senegalensis	7	21	31	7	66
S. africana	4	10	31	21	66
Z. mucronata	0	8	15	17	40
Total	**43**	**146**	**185**	**104**	**478**

Measuring browse production responses to defoliation

A plant may respond to herbivory via tolerance, avoidance (i.e. growing out of the herbivore's range), compensation, and/or induced defence (Gadd et al. 2001). Tolerance is defined by Gadd *et al.* (2001) as "a plant's ability to withstand and survive damage." Strauss and Agrawal (1999) define compensation to be "increased plant growth after loss of tissue to herbivores." When plant responses to herbivory are known to decrease herbivory rates, they are called induced defences (Owen-Smith 1993a, Karban and Baldwin 1997, Young and Okello 1998, Ward and Young 2002). Compensation for herbivory has been reported for *Acacias* (Milton 1988, Teague 1989, du Toit et al. 1990, Gadd et al. 2001) but few studies have been conducted on the response of other macrophyllous tree species to herbivory (O'Connor 1996). Where tree species use a mechanism of compensatory growth in the face of herbivory, protection from browsing may result in an under-estimation of actual shoot productivity, while the converse may also be true.

The effect of herbivory on production was investigated by the removal of leaf and green shoot material by hand, in such a way as to simulate the tearing and biting of leaves by browsing ungulates. For each tree species, half the numbers of individuals were defoliated at each quarterly measurement, i.e. the same individuals were defoliated at each quarter. All leaf and green shoot material was removed from a permanent variable width transect that ran the length of the tree canopy (top to bottom), excluding any tagged shoots within that transect. As shoot and leaf production declined in the dry season, so the transect width increased in order to maintain a constant weight of 100 g (wet weight) of browse removed.

Data analysis

Differences in annual browse production (kg/ha/annum) and seasonal browse production (kg/ha/quarter) among the different tree guilds, feeding levels and defoliation treatments were determined with paired samples t-tests, independent sample t-tests, one-way ANOVAs and repeated measures ANOVA (Genstat 9.1.0.147, Lawes Agricultural 2006) where appropriate. With repeated measurements, there is likely to be a greater correlation between observations that are made at adjacent time points than between those that are more greatly spaced (Payne et al. 2006). To correct for this correlation, a correction factor (epsilon), as described by Greenhouse and Geisser (1959), was applied.

Variation

The standard errors of the browse production estimates are relatively large (up to 80% of the mean in some cases). These large standard errors can be attributed to the considerable variances in mean shoot increments among and within each canopy stratum. By stratification, the total variance is reduced, but it is not inconsiderable. As a result of the large variances within samples, differences in browse production between years, quarters, feeding levels and defoliation treatments could not be established despite large differences existing between sample means.

Results

Browse production (differences between sampling years)

There was no difference in mean annual browse production (kg/ha/annum) between Year 1 (2003-2004) and Year 2 (2004-2005) for all seven savanna tree species studied (Table 4.3). The evergreen species, *E. divinorum*, recorded the greatest annual browse production (kg/ha/annum) over both years, with semi-deciduous species *S. africana* and *Z. mucronata* recording the second greatest production. Deciduous species *D. cinerea* and evergreen species *G. senegalensis* both recorded considerably lower annual browse production (kg/ha/annum) in comparison with their guild counterparts (*D. cinerea* approximately 85 times less than *A. nilotica* and *G. senegalensis* 25 times less than *C. bispinosa* and 55 times less than *E. divinorum)*.

Table 4.3: Mean browse production for deciduous, semi-deciduous and evergreen trees studied over two years along the northern Zululand coast of KwaZulu-Natal. Browse production values are based on a tree density of 1000 trees/ha. The t-value for a paired-samples 2-tail t-test is reported.

Species Guild	**Mean browse production (kg/ha/annum ± SE)**		**t-calc**	***P*-value**
	Year 1	**Year 2**		
Deciduous:				
Acacia nilotica	1760 ± 1347	2346 ± 1366	0.44	0.67
Dichrostachys cinerea	20 ± 10	28 ± 11	2.23	0.07
Mean	**1253.5 ± 960.7**	**1669.9 ± 984.0**	**0.44**	**0.66**
Semi-deciduous:				
Spirostachys africana	7587 ± 2696	5258 ± 1935	0.83	0.42
Ziziphus mucronata	7628 ± 1824	7250 ± 4012	0.10	0.92
Mean	**7603.4 ± 1744.3**	**6055.8 ± 1940.5**	**0.71**	**0.49**
Evergreen:				
Carissa bispinosa	4935 ± 1882	4893 ± 2338	0.03	0.98
Euclea divinorum	10720 ± 3306	13588 ± 5348	0.70	0.50
Gymnosporia senegalensis	192 ± 34.54	221 ± 77	0.36	0.72
Mean	**5499.9 ± 1448.7**	**6528.1 ± 2180.1**	**0.66**	**0.51**

Browse production differences between growing and non-growing seasons

The mean browse production (kg/ha/quarter) of *S. africana*, *Z. mucronata*, *C. bispinosa*, *E. divinorum* and *G. senegalensis* differed between growing and non-growing seasons. Despite the large differences in mean growing and non-growing season browse production of deciduous species (*A. nilotica* and *D. cinerea*), a significant result was not achieved due to the large sample standard errors (Table 4.4).

All tree species guilds showed the greatest mean browse production in the growing season. The largest difference in growing and non-growing season mean browse production was observed in deciduous *A. nilotica* (12 times greater) and semi-deciduous *S. africana* (8 times greater) and *Z. mucronata* (9 times greater). Although mean browse production was greater in the growing season (by a factor of three) in evergreen trees *C. bispinosa* and *E. divinorum*, *E. divinorum's* non-growing season production was greater than the other species.

Table 4.4: Mean growing and non-growing season browse production for each species guild studied over two years along the northern Zululand coast of KwaZulu-Natal. Browse production values are based on a tree density of 1000 trees/ha. The t-value for a paired-samples 2-tail t-test is reported.

Species Guild	**Mean browse production (kg/ha/quarter ± SE)**		**t-calc**	**P-value**
	growing season	**non-growing season**		
Deciduous:				
Acacia nilotica	1233 ± 721	100 ± 54	1.68	0.11
Dichrostachys cinerea	5 ± 3	8 ± 4	1.32	0.23
Mean	**875.1 ± 519.2**	**73.0 ± 39.7**	1.65	0.11
Semi-deciduous:				
Spirostachys africana	3662 ± 1153	444 ± 104	2.97**	0.01
Ziziphus mucronata	4337 ± 1449	462 ± 175	3.02**	0.01
Mean	**3932.2 ± 886.8**	**451.2 ± 92.5**	**4.28****	**0.00**
Evergreen:				
Carissa bispinosa	2384 ± 953	658 ± 287	2.40*	0.03
Euclea divinorum	5902 ± 1936	1610 ± 608	2.83*	0.01
Gymnosporia senegalensis	92 ± 28	31 ± 6	2.16*	0.05
Mean	**2917.1 ± 822.4**	**801.5 ± 251.1**	**3.34****	**0.00**

Quarterly browse production

Mean browse production (kg/ha/quarter) differed between sampling Periods in semi-deciduous and evergreen trees (Table 4.5). Mean browse production was greatest for all species (except *E. divinorum*) in sampling Period 2 (Oct-Dec 2003), followed by sampling Periods 5 (Jul-Sep 2004) and 6 (Oct-Dec 2004), the growing seasons as predicted by the CART® model presented in Chapter 3. Mean quarterly browse production (kg/ha/quarter) in evergreen species, *C. bispinosa* and *E. divinorum*, remained high across all of the sampling Periods, dipping only in the extreme dry season Period 4 (Apr-Jun 2004). The deciduous (*A. nilotica*) and semi-deciduous (*S. africana* and *Z. mucronata*) species showed a more seasonal browse production response with considerably lower browse production being recorded in the sampling Periods (Jul-Sep 2003, Jan–Mar 2004, Apr–Jun 2004, Jan–Mar 2005).

When looking at mean quarterly browse production as a proportion of annual production (%) for the three tree guilds, the strong seasonality of production in the deciduous and semi-deciduous trees studied is clear, with a single marked growing season being recorded for both guilds in both sampling years (Table 4.6). In the second sampling Period (Oct–Dec 2003), deciduous trees produced 92 % of their mean annual browse production; semi-deciduous trees produced 83 %, while evergreen trees only produced 56 %. In the second year, in the 5th sampling Period (Jul–Sep 2004), deciduous trees produced 59 % of their annual production, semi-deciduous trees interestingly only produced 10 % and evergreen trees 51 %. The semi-deciduous trees seemed to have a longer lag phase before the commencement of growth in the second sampling year, producing 79 % of their mean annual browse production in sampling Period 6 (Oct–Dec 2004).

Table 4.5: Mean browse production of three species guilds studied across 7 sampling seasons along the northern Zululand Coast of KwaZulu-Natal. Browse production values are based on a tree density of 1000 trees/ha. Letters above means indicate significant differences between seasons for each species guild (*P*<0.05).

Species	Mean quarterly browse production (kg/ha ± SE)							F-ratio	*P*-value
Guild	Jul-Sep 03	Oct-Dec 03	Jan-Mar 04	Apr-Jun 04	Jul-Sep 04	Oct-Dec 05	Jan-Mar 05		
	dry	dry	wet	dry	dry	wet	wet		
Deciduous:									
Acacia nilotica	55 ± 34	1625 ± 1319	74 ± 29	7 ± 3	1391 ± 889	684 ± 452	264 ± 170	$F_{6,96}$ = 1.38	0.27
Dichrostachys cinerea	5 ± 5	3 ± 3	12 ± 7	0 ± 0	0 ± 0	12 ± 6	16 ± 7	$F_{6,36}$ = 2.10	0.16
Mean	**40.3 ± 24.5**	**1151.8 ± 938.7**	**55.5 ± 21.3**	**5.0 ± 2.0**	**985.4 ± 637.8**	**488.1 ± 323**	**191.3 ± 121.5**	**$F_{6,138}$ = 1.37**	**0.27**
Semi-deciduous:									
Spirostachys africana	65^{a} ± 27	6524^{b} ± 2611	917^{c} ± 300	81^{a} ± 40	674^{ac} ± 400	3790^{b} ± 1491	714^{c} ± 215	$F_{6,84}$ = 4.84*	0.02
Ziziphus mucronata	0 ± 0	6158 ± 1470	1449 ± 722	21 ± 9	510 ± 307	6342 ± 4123	376 ± 262	$F_{6,54}$ = 3.03	0.10
Mean	**38.9^{a} ± 17.0**	**6377.5^{b} ± 1646.5**	**1130.1^{c} ± 335.1**	**56.9^{a} ± 24.5**	**608.4^{c} ± 266**	**4811^{b} ± 1842**	**578.7^{c} ± 166**	**$F_{6,144}$ = 7.78****	**0.00**
Evergreen:									
Carissa bispinosa	1409 ± 790	3057 ± 1165	426 ± 278	43 ± 17	1969 ± 994	2125 ± 1273	756 ± 405	$F_{6,90}$ = 2.55	0.07
Euclea divinorum	2589 ± 1359	5726 ± 2427	2245 ± 1382	160 ± 63	7508 ± 3560	4473 ± 2024	1447 ± 556	$F_{6,102}$ = 2.21	0.11
Gymnosporia senegalensis	7^{ac} ± 2	95^{b} ± 27	79^{bd} ± 24	10^{ac} ± 4	79^{abc} ± 42	102^{bd} ± 42	29^{cd} ± 9	$F_{6,90}$ = 2.65*	0.07
Mean	**1385.1^{a} ± 561.2**	**3070.1^{b} ± 989.0**	**969.9^{ac} ± 515.0**	**74.9^{c} ± 24.7**	**3358.3^{ab} ± 1374.6**	**2322.7^{ab} ± 858.5**	**772.2^{a} ± 248.3**	**$F_{6,294}$ = 3.45***	**0.02**

Table 4.6: Mean browse production and the proportion of the total annual browse production that each quarter accounts for is reported for three species guilds (Deciduous: *A. nilotica, D. cinerea*; Semi-deciduous: *S. africana*, *Z. mucronata*; Evergreen: *C. bispinosa*, *E. divinorum*, *G. senegalensis*), studied across 7 sampling seasons along the northern Zululand Coast of KwaZulu-Natal. Browse production values are based on a tree density of 1000 trees/ha.

		Deciduous		**Semi-deciduous**		**Evergreen**	
Quarter	**Season**	**Mean browse production (kg/ha ± SE)**	**Proportion of annual production (%)**	**Mean browse production (kg/ha ± SE)**	**Proportion of annual production (%)**	**Mean browse production (kg/ha ± SE)**	**Proportion of annual production (%)**
Jul - Sep 2003	Dry	40 ± 24	3	39 ± 17	0.5	1385 ± 561	25
Oct - Dec 2003	Dry	1152 ± 939	92	6378 ± 1647	84	3070 ± 989	56
Jan - Mar 2004	Wet	56 ± 21	4	1130 ± 335	15	970 ± 515	18
Apr - Jun 2004	Dry	5 ± 2	0.4	57 ± 24	0.7	75 ± 25	1
Annual total		**1252.5 ± 959.7**		**7603.4 ± 1744.3**		**5499.9 ± 1448.7**	
Apr - Jun 2004	Dry	5 ± 2	0.3	57 ± 24	1	75 ± 25	1
Jul – Sep 2004	Dry	985 ± 638	59	608 ± 266	10	3358 ± 1375	51
Oct – Dec 2004	Wet	488 ± 323	29	4811 ± 1842	79	2323 ± 859	36
Jan – Mar 2005	Wet	191 ± 121	11	579 ± 166	10	772 ± 248	12
Annual total		**1669.9 ± 984.0**		**6054.8 ± 1940.5**		**6528.1 ± 2180.1**	

Stratified browse production (annual differences)

The mean annual browse production (kg/ha/annum) of the different feeding levels in the tree canopy differed in deciduous *D. cinerea* and semi-deciduous *Z. mucronata*, although these results were not consistent over sampling years (Table 4.7). Mean annual browse production for all three tree guilds was consistently greater at each level moving higher in the canopy, with the greatest production being recorded in the highest feeding level (2.5-5.0m) and the least in the lowest feeding level (0.0-0.5m).

Stratified browse production (differences in cumulative mean quarterly production)

Only small differences between the cumulative mean browse production (kg/ha/quarter) of the different feeding levels of deciduous *A. nilotica* were observed during study Year 1, with large standard errors (a). Differences between the cumulative mean browse production of the different feeding levels of deciduous *A. nilotica* are more pronounced during study Year 2, although the large standard errors remain. The largest difference is observed between the cumulative mean browse production of feeding level 2.5-5.0 m and the other feeding levels combined at the start of the growing season (Jul-Sep 2004). Deciduous *D. cinerea* showed no real differences in cumulative mean browse production between the different feeding levels during study Year 1, until the end of the growing season (Oct-Dec 2003). By the end of the first growing season, the difference between the production of feeding level 2.5-5.0 m was greater than that for the other feeding levels (b), although large standard errors remained. After leaf fall (Apr-Jun 2004), during the second study year, larger differences were observed in the cumulative mean quarterly browse production between the different feeding levels of *D. cinerea*, especially after the prolonged growing season (Jul-Dec 2004).

Table 4.7: Mean browse production for of three species guilds studied across 7 sampling seasons along the northern Zululand Coast of KwaZulu-Natal. Browse production values are based on a tree density of 1000 trees/ha. Letters above means indicate significant differences between seasons for each species guild (*P*<0.05).

Species Guild	**Year**	**Mean browse production for each feeding level (kg/ha/annum ± SE)** 0.0-0.5 m	0.5-1.5 m	1.5-2.5 m	2.5-5.0 m	**F-ratio**	***P*-value**
Deciduous:							
Acacia nilotica	1		246 ± 144	710 ± 410	1499± 1122	$F_{2,38} = 0.85$	0.44
	2		64 ± 36	1036 ± 493	3157 ± 2374	$F_{2,38} = 1.33$	0.28
Dichrostachys cinerea	1		4 ± 3	8 ± 5	39 ± 25	$F_{2,11} = 3.32$	0.07
	2		3^{a} ± 2	13^{a} ± 5	56^{b} ± 24	$F_{2,11} = 8.52$**	0.01
Mean	**1**		**161.1 ± 95.7**	**562.0 ± 328.2**	**1224.9 ± 916.2**	**$F_{2,52} = 1.09$**	**0.34**
	2		**42.8 ± 24.0**	**821.0 ± 398.7**	**2575.4 ± 1939.5**	**$F_{2,52} = 1.59$**	**0.21**
Semi-deciduous:							
Spirostachys africana	1	729 ± 530	1355 ± 742	1756 ± 401	6045 ± 3094	$F_{3,29} = 1.35$	0.28
	2	344 ± 335	762 ± 722	1055 ± 352	1735 ± 621	$F_{3,29} = 0.84$	0.49
Ziziphus mucronata	1		199^{a} ± 184	1575^{ab} ± 638	5892^{b} ± 1876	$F_{2,20} = 4.68$*	0.02
	2		20.94 ± 16	2700 ± 2284	1933 ± 782	$F_{2,20} = 0.55$	0.58
Mean	**1**	**729.1^{ab} ± 530.1**	**776.7^{a} ± 408.5**	**1685.3^{a} ± 340.7**	**5976.4^{b} ± 1854.5**	**$F_{3,52} = 3.53$***	**0.02**
	2	**344.1 ± 334.6**	**391.7 ± 362.1**	**1698.6 ± 903.5**	**1824.4 ± 477.4**	**$F_{3,52} = 0.65$**	**0.59**
Evergreen:							
Carissa bispinosa	1	902 ± 432	4049 ± 1863	4230 ± 2998		$F_{2,31} = 0.95$	0.40
	2	1363 ± 1067	3032 ± 1888	4126 ± 3261		$F_{2,31} = 0.40$	0.68
Euclea divinorum	1	969 ± 526	3451 ± 1496	3584 ± 1598	6339 ± 2362	$F_{3,46} = 0.97$	0.42
	2	895 ± 760	5661 ± 2290	4029 ± 1495	8917 ± 6748	$F_{3,46} = 0.70$	0.55
Gymnosporia senegalensis	1	6 ± 5	94 ± 60	39 ± 12	92 ± 71	$F_{3,34} = 0.68$	0.60
	2	10 ± 9	58 ± 27	127 ± 50	289 ± 243	$F_{3,34} = 1.44$	0.25
Mean	**1**	**750.4 ± 274.3**	**2663.4 ± 857.6**	**2356.6 ± 910.1**	**4256.5 ± 1735.3**	**$F_{2,118} = 1.264$**	**P=0.290**
	2	**971.7 ± 593.8**	**3109.4 ± 1086.2**	**2560.8 ± 912.5**	**6040.9 ± 4549.8**	**$F_{2,118} = 1.122$**	**P=0.343**

For semi-deciduous species, *S. africana* and *Z. mucronata*, minimal production was recorded across all feeding levels during the non growing season (Jul-Sep 2003) in Year 1 (Figure 4.2a&b). Divergence between the cumulative mean browse production of the different feeding levels occurs after the growing season (Oct-Dec 2003), with the most pronounced difference being between the 2.5-5.0 m feeding level and the rest of the lower tree canopy. During Year 2, the differences between the cumulative mean browse production of the different feeding levels are less pronounced for both species. Interestingly, during the second study year, the 1.5-2.5 m feeding level recorded the greatest production comparatively in *Z. mucronata*, the only instance of this occurrence.

In evergreen species *C. bispinosa, E. divinorum* and *G. senegalensis,* the lowest feeding level (0.0-0.5 m) consistently produced the lowest cumulative mean browse production across both study years and seven sampling seasons when compared to the other feeding levels (Figure 4.3a,b&c). Differences in the cumulative mean browse production among feeding levels was small for all evergreen species in Year 1, with large and overlapping standard errors. These differences were more pronounced during Year 2 (although large standard errors remained), with the largest difference being observed in *G. senegalensis* between the 2.5-5.0 m feeding level and the other feeding levels at the start of the growing season (Jul-Dec 2004) (Figure 4.3c).

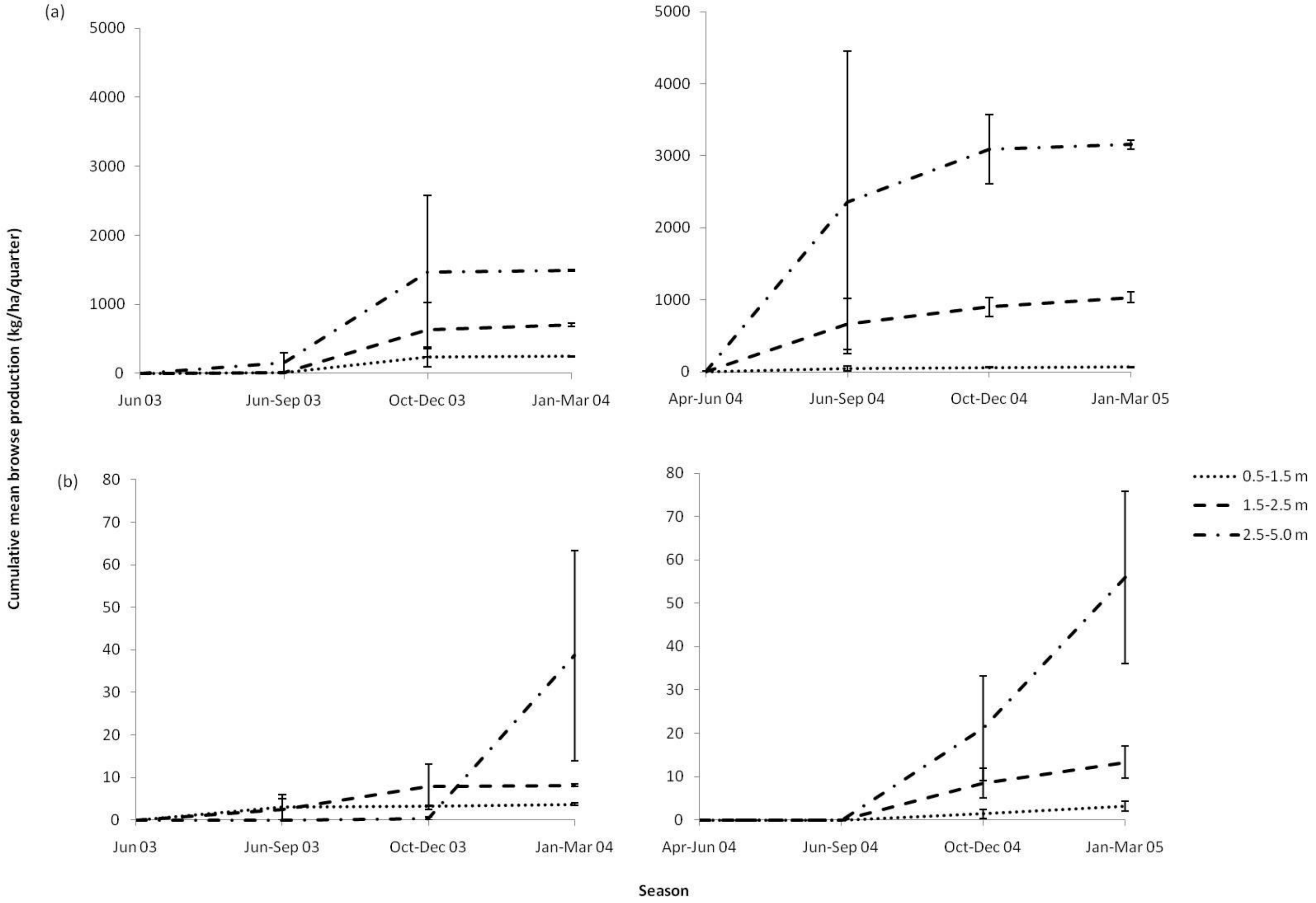

Figure 4.1: A comparison of mean browse production for different feeding levels for deciduous trees, for (a) *A. nilotica* and (b) *D. cinerea* studied over two years of tagged shoots across seven sampling seasons along the northern Zululand coast of KwaZulu-Natal

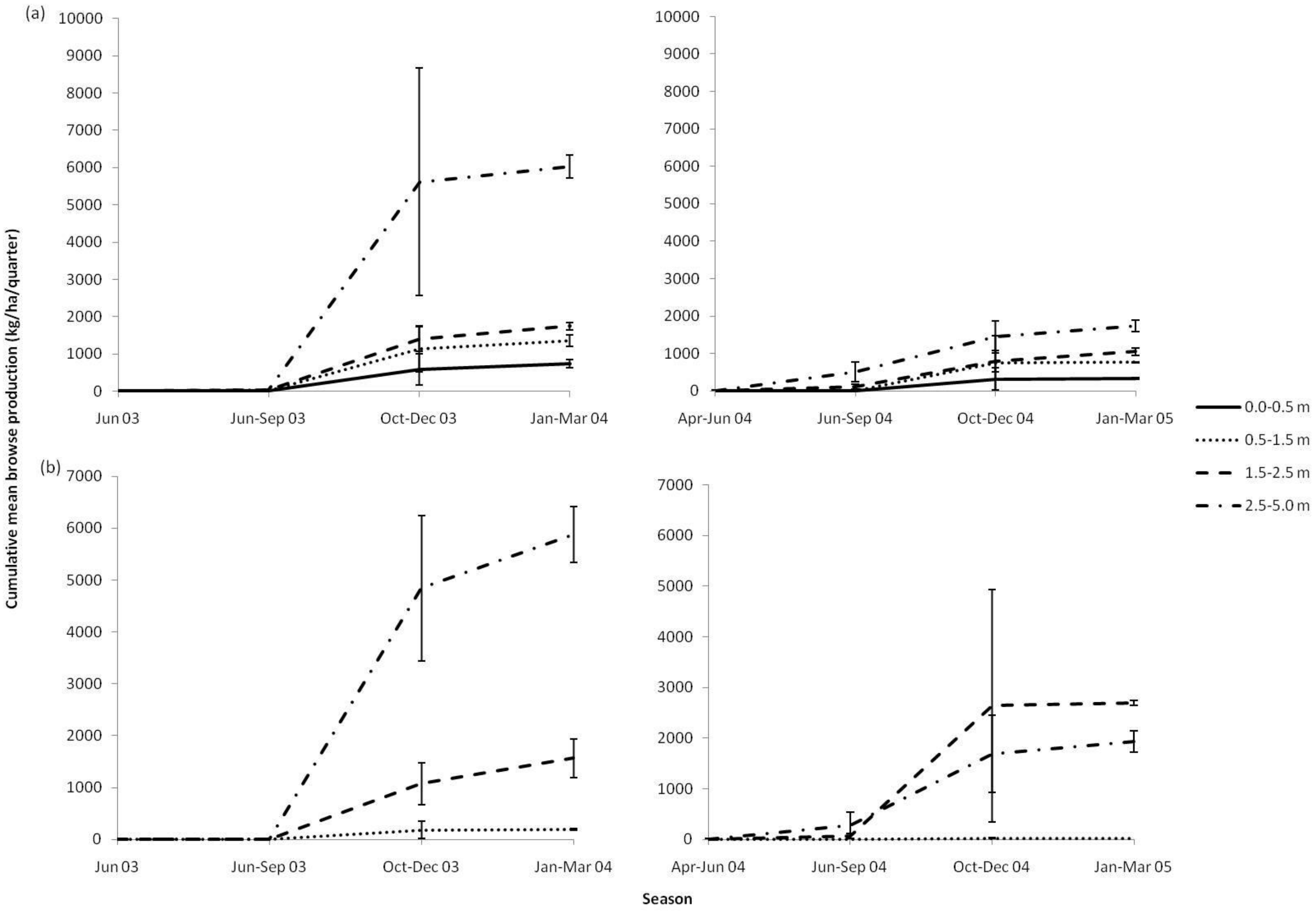

Figure 4.2: A comparison of mean browse production for different feeding levels for semi-deciduous trees, for (a) *S. africana* and (b) *Z. mucronata* studies over two years of tagged shoots across seven sampling seasons along the northern Zululand coast of KwaZulu-Natal.

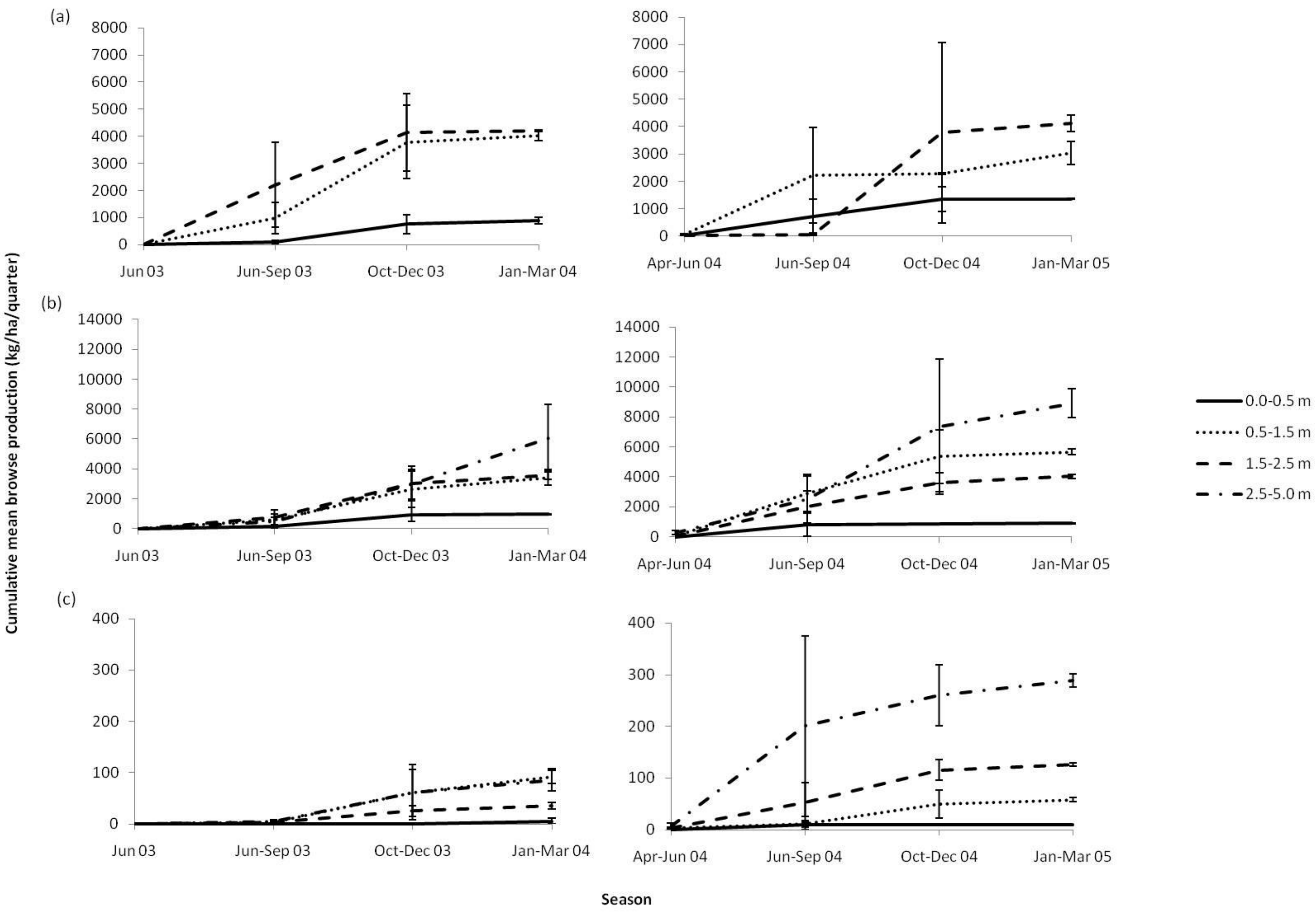

Figure 4.3: A comparison of mean browse production for different feeding levels for deciduous trees, for (a) *C. bispinosa*, (b) *E. divinorum* and (c) *G. senegalensis* studied over two years of tagged shoots across seven sampling seasons along the northern Zululand coast of KwaZulu-Natal.

Effect of defoliation on browse production

Because of the large variances in shoot increments, differences between the mean browse production (kg/ha/annum) of trees that underwent quarterly simulated browsing and trees that did not were apparent, even after two year's growth (Table 4.8). This result was consistent across all seven tree species and both study years.

Table 4.8: Mean browse production with and without defoliation for key browse species, with t- and *P*-values, studied over two years of tagged shoots across seven sampling seasons along the northern Zululand coast of KwaZulu-Natal. Browse production values are based on a tree density of 1000 trees/ha. The t-value for an independent samples 2-tail t-test is reported.

Species	**Year**	**Mean browse production (kg/ha/annum ± SE)**		**t-calc**	***P*-value**
		quarterly defoliation	**no defoliation**		
Acacia nilotica	1	5467 ± 3308	4155 ± 1607	1.45	0.17
	2	197 ± 74	34 ± 15	1.94	0.07
Carissa bispinosa	1	7470 ± 2731	7210 ± 3941	2.59*	0.02
	2	474 ± 322	1489 ± 1108	1.40	0.18
Dichrostachys cinerea	1	1 ± 0.2	20 ± 12	0.82	0.44
	2	22 ± 13	23 ± 12	0.12	0.91
Euclea divinorum	1	14591 ± 3930	19400 ± 9061	1.86	0.08
	2	5229 ± 2985	5621 ± 2890	1.38	0.18
Gymnosporia senegalensis	1	190 ± 75	343 ± 156	0.17	0.87
	2	176 ± 43	102 ± 48	2.07*	0.06
Spirostachys africana	1	5245 ± 2149	6026 ± 2821	0.29	0.78
	2	6531 ± 3496	2788 ± 844	1.26	0.23
Ziziphus mucronata	1	8782 ± 1971	4505 ± 1502	1.44	0.18
	2	4046 ± 22638	7139 ± 5990	0.36	0.73

The effect of defoliation on browse on production was differed among tree guilds (Figure 4.4, Figure 4.5, Figure 4.6). In deciduous (*A. nilotica*) and semi-deciduous (*S. africana* and *Z. mucronata*) trees, the response to defoliation, during the first year, was concentrated in the growing season (Oct-Dec 2003), while evergreen trees (*C. bispinosa* and *E. divinorum*) showed an immediate favourable response to defoliation. During the second year of study, browse production response to defoliation occurred a season earlier in all evergreen trees (*C. bispinosa*, *E. divinorum* and *G. senegalensis*), in semi-deciduous *S. africana* and in deciduous *A. nilotica*.

Defoliation stimulated browse production in *A. nilotica* (Figure 4.4a), *C. bispinosa* (Figure 4.6a) and *E. divinorum* (Figure 4.6b) across both study years.

S. africana (Figure 4.5a) and *G. senegalensis* (Figure 4.6c) only showed a favourable response to defoliation during the second year, while *Z. mucronata* showed stimulated browse production in Year 1 as a result of defoliation, with defoliation having a negative effect on production in Year 2 (Figure 4.5b). Browse production was retarded by defoliation in *D. cinerea* across both study years (Figure 4.4b).

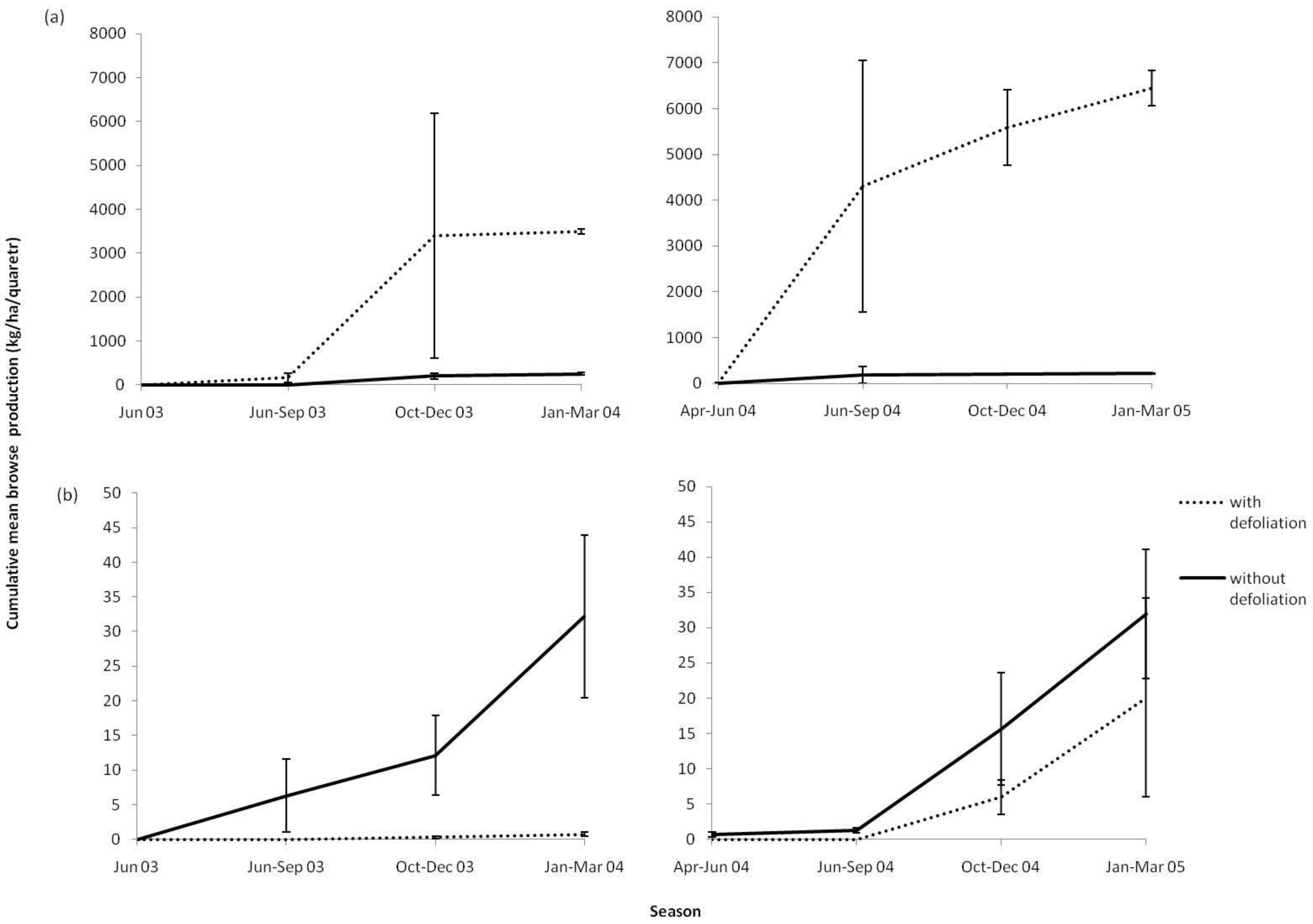

Figure 4.4: A comparison of tagged shoots mean browse production with and without defoliation (with standard errors), for deciduous trees (a) *A. nilotica* and (b) *D. cinerea* studied over two years, across seven sampling seasons along the northern Zululand coast of KwaZulu-Natal.

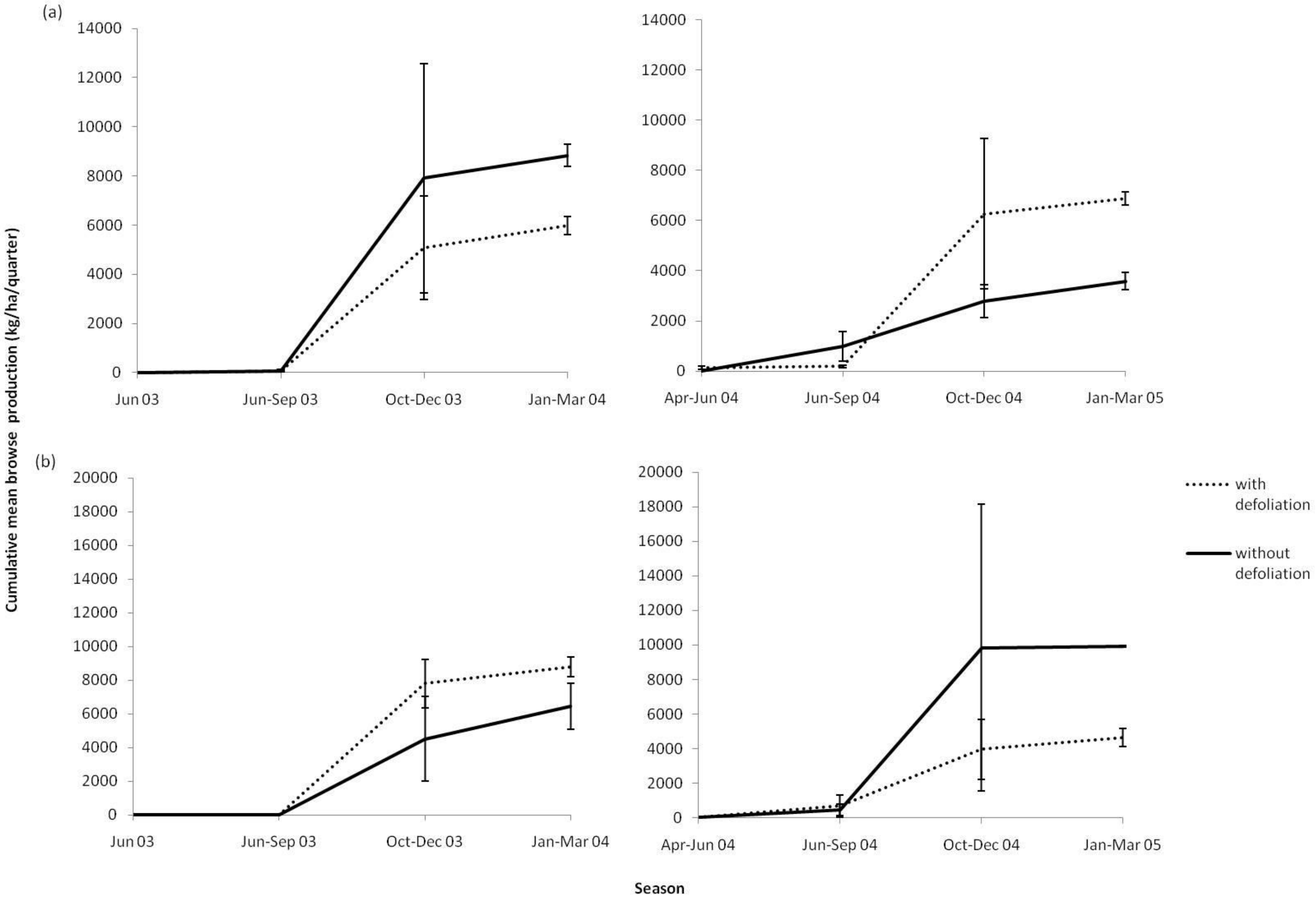

Figure 4.5: A comparison of tagged shoots mean browse production with and without defoliation (with standard errors), for semi-deciduous trees, for (a) *S. africana* and (b) *Z. mucronata* studied over two years, across seven sampling seasons along the northern Zululand coast of KwaZulu-Natal.

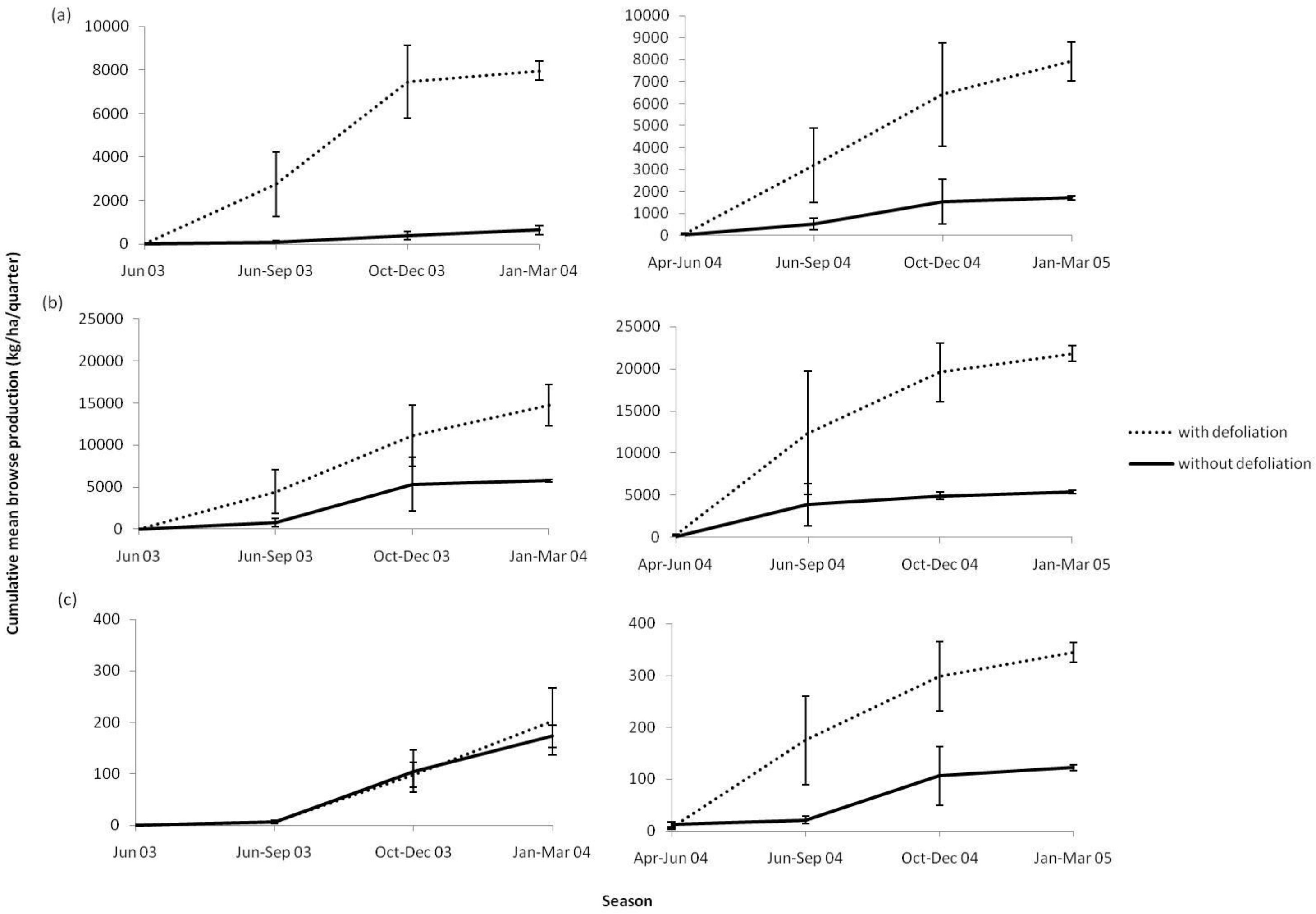

Figure 4.6: A comparison of tagged shoots mean browse production with and without defoliation (with standard errors), for evergreen trees (a) *C. Bispinosa*, (b) *E. Divinorum* and (c) *G. senegalensis* studied over two years, across seven sampling seasons along the northern Zululand coast of KwaZulu-Natal.

Discussion

Differences in browse production between species guilds

Evergreen trees (with the exception of *G. senegalensis*) consistently maintained greater browse production than deciduous trees across both study years and all seven sampling seasons. Browse production, in this study, is based on increments in shoot length (Chapter 3). In deciduous species like *A. nilotica*, much of the investment of energy during the growing season is in the production of new leaves – often on existing, woody, lignified branches (Milton 1987). Proportionally less energy is available therefore, for vertical or horizontal canopy growth and shoot extension.

Another consideration is the differences in canopy shape, depth and volume between the different study trees. Since ACVol (defined in Chapter 3) is used in the calculation of browse yields, these differences are important. Considerably less surface area of browse is accessible to browsing ungulates on the typical umbrella shaped canopy of *Acacias* than the more rounded canopy of species, such as *Z. mucronata* or *E. divinorum* (Archibald and Bond 2003). Further, both *C. bispinosa* and *E. divinorum* recorded relatively greater production than *G. senegalensis*. This difference may be explained by differences in the canopy structure between the species, where *Carissa* and *Euclea* species are multi-stemmed trees with canopies consisting of a dense network of branches of different sizes and ages. Shoots themselves are often much branched, resulting in a greater number of potential browse production sites. The canopy of *G. senegalensis* on the other hand, is a somewhat looser network of branches, with single unbranched shoots produced on branching tips. The potential browse production per unit ACVol is therefore an important consideration in determining browse production of tree communities and browser carrying capacities.

Semi-deciduous trees, on average, recorded the greatest mean quarterly browse production in the growing season for both study years, producing at least double that of evergreen trees. Conversely, deciduous trees, on average, recorded the lowest mean quarterly browse production during the growing season. This is largely because of the long season of deciduousness experienced by these species, which lowers the overall comparative annual yield of this guild.

Deciduous species also tend to invest more energy into leaf production, on old existing branches, than in shoot extension (Milton 1987).

The semi-deciduous species *S. africana* and *Z. mucronata* produced proportionally more browse, across all study areas, than both the deciduous and the evergreen guilds, during the growing season. Both *Z. mucronata* and *S. africana* favour water-rich soils, and often occur along drainage lines and river banks (Pooley 1997), as was the case in our study. Browse production in these species is therefore enhanced by greater soil moisture content (Do et al. 2005). Greater rates of production in *S. africana* and *Z. mucronata* compared with *A. nilotica* may also be a function of canopy architecture differences between the species. The ACVol of *S. africana* and *Z. mucronata* is greater than that of *A. nilotica* (Archibald and Bond 2003).

The seasonality of browse production was discussed at length in Chapter 3 and will not be repeated here. What is important, in terms of this study, are the differences in growing season length between evergreen and deciduous species. Deciduous trees tend to concentrate their growth in a single short period, when growing conditions are favourable. Microphyllous, deciduous trees, like *Acacias*, have been documented to be fast-growing, high-resource-adapted plants (Coley et al. 1985, Bryant et al. 1989, Skowno et al. 1999, Smit 2003, Midgley and Bond 2001, Milton 1987). Evergreen species, by contrast are often referred to as being slow-growing, long-lived plants (Skowno et al. 1999). While they do experience a period of heightened growth, initiated just prior to the wet season, under favourable conditions, they are able to maintain browse production for longer periods during the year. The importance of this continued production, in terms of browsing ungulate management, is that new shoot material is available for browsers throughout the year, even in the dry season.

Differences in browse production between feeding levels

All three tree guilds produced consistently greater amounts of browse up the canopy, with the 2.5-5.0 m feeding level recording the greatest browse production and the 0.0-0.5 m feeding level the least. Few trees produced leaves at the 0.0-0.5 m level, while any leaves and shoots that are produced have to contend with shading from the above canopy, resulting in lower production rates for this feeding level. Bearing in mind that this study was conducted in the absence of browsing, and that the browse production did not include compensatory growth, the fact that the greatest browse production was recorded for the 2.5-5.0 m feeding level may be pertinent. Perhaps, when not taxed by efforts to continuously replace material removed by browsing at herbivore browsing levels, tree species concentrate production in areas of maximum light interception to increase rates and assimilation of photosynthates.

The effect of defoliation on browse production

The response of leaf and shoot growth to defoliation has been relatively well investigated for the genus *Acacia* but almost ignored for deciduous and evergreen broad-leafed species (O'Connor 1996). All African *Acacia* species studied so far have shown compensatory growth in response to defoliation: *A. nigrescens* (du Toit et al. 1990), *A. karroo* (Stuart-Hill and Tainton 1988, Teague and Walker 1988a, Teague 1989), *A. tortilis* (Milton 1988, Pellew 1983a, du Toit et al. 1990). The only example in which browsing had an inhibitory effect on production was for two West African species, *Combretum apiculatum* (macrophyllous) and *Cadaba farinose* (evergreen) (Cissé 1980). Although no difference could be reported between mean annual browse production with and without defoliation for *A. nilotica, C. bispinosa, D. cinerea, E. divinorum, G. senegalensis, S. africana,* and *Z. mucronata*, the response of leaf and shoot growth of these species to defoliation follows similar trends to that reported in literature, with deciduous trees, *A. nilotica* and *D. cinerea*, exhibiting compensatory growth, as well as increased growth rates when defoliated. The only tree to exhibit a negative response to simulated browsing was *D. cinerea*. This may have been due to the fact that all the study trees of this species were of a similar age and size, with few individuals being taller than 2 m. All individuals had suffered heavy browsing during the dry years prior to the commencement of the study.

Pruning or defoliation early in the growing season, when stored carbohydrates have been expended to produce leaves and shoots in spring, reduces the productivity of trees (Menke and Trlica 1981). Repeated harvesting or continuous browsing has been shown to reduce browse production of *A. karroo* in the Eastern Cape (Aucamp and Tainton 1984), and *Acacia* spp. and broad-leafed species in the Sahel (Cissé 1980). In our study, the effect of defoliation on browse production was greater during the growing season, than in any other season, and had a lasting effect on cumulative browse production over the rest of the year.

Implications of dry season browse production on carrying capacity determinations

As a result of the structural differences between the evergreen trees and deciduous trees and in response to their different strategies to coping with periods of low rainfall, evergreen trees (through the retention of leaves year round) have a greater potential browse biomass than do their deciduous counterparts. The extreme of this difference occurred during the dry season, when complete deciduousness is achieved and no browse biomass on these trees is available to browsing ungulates. The implication of this for management of savanna trees and management of browse forage for herbivores, is that, during the dry winter period, only evergreen leaf material is available for consumption, if all deciduous trees achieve complete deciduousness (i.e. lose all their leaves). During the growing season, when leaf and young shoot material (i.e. browse production) is available on the more palatable deciduous species, evergreen trees generally, are selected against, suffering only very moderate levels of browse intensity. In more arid areas, this situation is potentially reversed during the dry season. Due to the greater energy costs of maintaining leaves during the dry season, intense and frequent dry season defoliation may have a detrimental effect on the ability of evergreen trees to initiate new growth during the following season. Consequently, evergreen stands exposed to high animal densities, in more arid areas, may be artificially contained in small patches, resulting in greater densities of deciduous trees (having avoided dry season browsing by dropping all their leaves). Another result of this unequal browse pressure may be more open savanna areas.

An alternate situation may arise, where ‘deciduous’ trees only reach a state of semi-deciduousness, as in the case of *S. africana* and *Z. mucronata* in our study. Since (semi-)deciduous trees are more palatable and generally more strongly selected for than evergreen trees, they may be exposed to greater browsing pressure during the winter dry season, when other forage resources are limiting. Mixed feeders switch from grass to browse during the dry season (Owen-

Smith 2008). Unlike grass, woody foliage retains consistent water content throughout the seasonal cycle, which enables savanna browsers to be largely independent of surface drinking water (Western 1975). Maintaining a balance of deciduous and evergreen browse species is therefore important to maximising browser carrying capacity.

Conclusion

Measurement of browse production of key deciduous, semi-deciduous and evergreen tree species common along the northern Zululand Coast of KwaZulu-Natal, allowed for broader understanding of browse dynamics in southern Africa. Differences in browse production among tree guilds were observed, with mean annual browse production following the trend: semi-deciduous trees > evergreen trees > deciduous trees. The seasonality of browse production was well documented, with evidence that all three tree guilds experience a distinct growing season (which was initiated during the sampling Period prior to the start of the wet season). Browse production of deciduous and semi-deciduous trees during the non-growing season was less than that of evergreen trees, which are able to maintain browse production for longer periods (during unfavourable conditions) during the year. Annual browse production at the different tree canopy feeding levels for all tree guilds followed the trend: 0.0-0.5 m > 0.5-1.5 m > 1.5-2.5 m > 2.5-5.0 m. In the absence of browsing, browse production was focused in areas of maximum light interception to increase rates and assimilation of photosynthates, allowing the tree to grow taller. Finally, the moderate level of defoliation improved browse production for all tree guilds. This chapter, together with Chapter 3, draws attention to the large inherent variability in browse production measurements (Pellew 1983a, Bille 1980). The result of this variability is that when traditional parametric statistical comparison tests are used, few differences are established between samples/treatments despite large differences between sample/treatment means. Despite this, it is clear that inherent variability is a key factor in browse system functioning, and is extremely important for system resilience and robustness. We must, therefore, not simply try to explain it, but rather grapple with it in model building and in understanding how browse production, and browse systems, as a whole, function. Regression trees are one such tool that are able to deal with inherent variability.

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CHAPTER 5. RELATION BETWEEN BROWSE PRODUCTION AND NUTRITIVE VALUE IN THREE TREE SPECIES GUILDS IN NORTHERN ZULULAND

“Part of the secret of success in life is to eat what you like
and let the food fight it out inside”
M. Twain

Abstract

Browse selection, intake, utilisation, palatability, nutritive value and production are tightly linked and need to be considered together in trying to improve our understanding of browsing dynamics. Such understanding is required in order to re-evaluate determinations of browser carrying capacities and to evaluate actual and potential impacts of browsing animals on vegetation. This study investigated the relation between the palatability and nutritive value of six key savanna tree species, common along the northern Zululand coast of KwaZulu-Natal in order to relate these findings to the annual growth rates of these species. The study further aimed to determine whether the nutrient levels of woody plants that are utilised by browsing herbivores were sufficient to supply the daily nutrient requirements of these herbivores throughout the year.

Browse nutritive value was found to be greatest during the wet season, when growth and photosynthesis are at their peak. Further, browse nutritive value was greatest in deciduous species. Evergreen trees across all three study areas had greater acid detergent fibre (ADF) concentrations than the deciduous and semi-deciduous trees, although these differences were not consistent. By contrast, crude protein (CP) concentrations were greater in semi-deciduous and deciduous species (across all three study areas) than in evergreen species.

Browse production was positively correlated with concentrations of CP below 10.4 %, concentrations of phosphorus above 0.1 % and concentrations of calcium below 1.1 %. Likewise, lower levels of browse production were positively correlated with greater concentrations of ADF.

The daily CP requirements for maintenance for an adult impala (45 kg) were met by all species over all three study areas and all seven Period. Daily CP requirements for growth and lactation, however, were only met by deciduous and semi-deciduous species, though this was not consistent over study areas and years.

The maintenance of sustainable browsing herbivore populations requires a habitat with a diverse range of browse species (including deciduous, semi-deciduous and evergreen species) to meet the year-round nutritional requirements of the animals.

Introduction

Large herbivores are often simplistically classified into two groups, namely grazers and browsers, according to the plant groups that make up the majority of their diet (Bergström 1992). This classification is supported by Hofmann and Stewart (1972) as well as Hofmann (1989) who suggested that the major dichotomy separating species of ruminants is their adaptations for consuming a bulk/roughage diet of primarily grasses (grazers) or a concentrate diet of browse or forbs (browsers). A ‘concentrate selector’ or ‘browser’ is defined by Hofmann and Stewart (1972) as “a ruminant that selects a diet containing at least 75% fruits, dicotyledonous foliage, and tree and shrub stems and foliage.” Bodmer (1990) and Robbins *et al.* (1995), among others, have argued that tree and shrub foliage should not be considered as ‘concentrates’, as they often contain high concentrations of plant secondary compounds and lignin. True concentrate feeders and browsers should therefore form separate categories (Bodmer 1990). Others argue that these feeding categories rather reflect trends in body mass and metabolic requirements as smaller herbivores tend to select concentrates whereas larger ones tend to choose roughage or grass (Gordon and Illius 1994, Robbins et al. 1995). This argument fails however, in terms of placing black (browser) and white (grazer) rhino into feeding categories.

Whether dietary selection is attributed to body size (Bell 1971, Jarmen 1974), energy constraints (Mentis and Duke 1976), physiological adaptations (Hofmann and Stewart 1972), niche separation, competitive exclusion (Illius and Gordon 1993) or predation (Sinclair 1995), browsing herbivores are faced with a more heterogeneous assembly of plant community structures, plant species and plant parts of various nutritional value than grazing herbivores face. Generally browse plants have greater levels of cell concentration, lignin, secondary compounds and nitrogen than do grasses (Shipley 1999a). By feeding on plant parts with high lignin and secondary compound concentration, a browsing herbivore is often unable to assimilate enough protein for its maintenance requirements. Browsing herbivores are then forced to select for components of the vegetation available to them that have thin cell walls, limited chemical defences and high concentrations of protein, such as new leaves, green shoots and fruits (Bell 1971, Jarmen 1974). Browse selection is usually limited to the current season's growth or browse production (defined Chapter 3). The extent of browse or 'concentrate' selection that is undertaken is in turn related to body size, morphological feeding adaptations and the vegetation on offer.

The proportion of woody vegetation made up of green leaves and new twigs is generally small (Walker 1980). This is largely a result of three factors: (1) Due to the effects of apical dominance in woody species, new growth is only added at the branch tips (Novoplansky 2003). (2) Many woody species also have spines, thorns, or short, stubby branches that slow or inhibit cropping (Cooper and Owen-Smith 1986). (3) Woody species tend to be more discrete in their dispersion compared to grasses (Scholes and Archer 1997, Shipley 1999b). In addition, often only a relatively small proportion of these leaves and twigs are actually available to browsing ungulates due to tree size, position and density. Browsers in Africa seldom use >10% of the standing plant biomass in any area (Owen and Wiegert 1967, von Holdt 1999) even during the resource limiting periods of the year. In fact some studies have shown utilisation percentages to be as low as 2% of the standing browse biomass (Owen-Smith 1985).

Because, according to Pietersen *et al.* (1993), the principal factor in the calculation of carrying capacity estimates is forage intake, browsing capacity estimates depend not only on browse production, but also on the fraction of this available biomass that is eaten. Because woody species vary widely in their utilization by browsing herbivores, it is common practice when assessing available forage biomasses for carrying capacity determination to assign species to palatable and unpalatable categories (Barnes et al. 1984, Owen-Smith and Cooper 1988) (Chapters 3, 4 and 6). Owen-Smith and Cooper (1987a) proposed a palatability classification of woody species in which palatable species are those remaining highly acceptable during all seasons, as long as they retain leaves. Unpalatable species are largely rejected in the late wet season when plant foliage is most abundant. Unpalatability is determined by the nutrient concentrations or textual properties of leaves, including: (a) protein and various mineral elements; (b) cellulose, hemicelluloses and lignin; and (c) plant secondary metabolites (Owen-Smith and Cooper 1987a). Browse selection, intake, utilisation, palatability, nutritive value and production are tightly linked and need to be considered together when attempting to improve our understanding of browsing dynamics, in order to re-evaluate determinations of browser carrying capacities and evaluating actual and potential impacts of browsing animals on vegetation.

The aim of this chapter was primarily to investigate the relation between the palatability and nutritive value of six key savanna tree species common along the northern Zululand coast of KwaZulu-Natal and then relate these findings to the annual browse production of these species. It was hypothesized that browse nutritive value (as defined by the relative concentrations of favourable plant nutrients for herbivore consumption) and browse palatability (herbivore selection) are strongly correlated and in turn are related to browse production. Specifically my objectives were: (a) to relate the nutrient characteristics of the different tree species to known browser selection patterns, with the prediction that tree species with greater digestible nutrient concentrations will be those species that are more highly selected for by large browsing herbivores; (b) to investigate the influence of seasons and study area on browse nutritive value, with the prediction that browse nutritive value will be greatest during wetter seasons in drier study areas; (c) to determine whether a relation exists between browse production and browse nutritive value, with the prediction that species that show high browse production rates will also have high concentrations of favourable nutrients (plant nutrients); and lastly (d) to determine whether the nutrient concentrations of woody plants that are utilised by browsing herbivores met the daily nutrient requirements of these herbivores. The investigation of these questions should develop our understanding of the dynamics of browse production and browser selection among woody plants in semi-arid, subtropical savannas. Such knowledge would be useful for guiding management-orientated modelling of browse-browser interactions in seasonal, subtropical zones in southern Africa where wild browsers are abundant and managers need to determine browser carrying capacities, as well as evaluating impacts of browsing animals on vegetation.

Procedure

Study areas and species selection

Browse nutritive value was investigated over two years with very different rainfall (June 2003 - April 2004 (below average) and June 2004 - April 2005 (above average)) in three game reserves, namely Bonamanzi Game Park (BGP), Mun-Ya-Wana Private Game Reserve (MGR) and Pongola Game Reserve (PGR), situated on an approximately north/ south axis in northern Zululand, along a distinct rainfall and temperature gradient.

Browse nutritive value was determined for six key tree species, representing three guilds: deciduous - *Acacia nilotica*; semi-deciduous - *Spirostachys africana* and *Ziziphus mucronata*; and evergreen - *Carissa bispinosa*, *Euclea divinorum* and *Gymnosporia senegalensis*. These species were chosen because they represent a range of palatability to ungulates and leaf sizes (Table 3.1), were common, and occurred at high densities across all three study areas.

Data collection and analysis

Nutrient status of the available browse of the study tree species were determined from shoot samples (leaves and green twigs), collected by hand to simulate browser feeding. Samples were collected for seven sampling Periods (1 = Jul 03 – Sept 03; 2 = Oct 03 – Dec 03; 3 = Jan 04 – Mar 04; 4 = Apr 04 – Jun 04; 5 = Jul 04 – Sep 04; 6 = Oct 04 – Dec 04; 7 = Jan 05 – Mar 05). Only the current season's growth (soft green shoots, leaves and buds) was sampled as this material was most likely to be selected by browsing herbivores (Walker 1980). All samples were collected within fenced exclosure plots (defined in Chapter 3). For each tree species, half the numbers of tagged individuals (3-4 individuals/species/study area (Table 3.2)) within the exclosure plots were harvested in a manner similar to browsing during each sampling period (defined in Chapter 4), i.e. the same individuals were defoliated at each quarterly sampling. All leaf and green shoot material was removed from a variable width transect that ran the length of each tree canopy (top to bottom), excluding any tagged shoots within that transect. As shoot and leaf production declined in the dry season, so the transect width increased in order to maintain a constant weight of 100 g (wet weight) of new leaf and shoot material being removed at each quarter. At each quarterly measurement, a proportion of the new growth was removed by hand, in such a way as to simulate the tearing and biting of leaves by browsing ungulates, oven-dried at 70^{o}C to a constant weight, and milled.

Analyses for nutrients and fibre components were done by the Cedara Feed Laboratories in Pietermaritzburg. Samples were analysed for crude protein (CP) , acid digestive fibre (ADF), phosphorus (P), potassium (K) and calcium (Ca) and expressed as a percentage of total dry matter (% DM). These nutrient characteristics were chosen as together they provide the best indication of browse palatability. (1) Crude protein is derived from a measure of nitrogen x 6.25. Crude protein, as a measure of nutritive value, is used most widely from the perspective of animal nutrition, while nitrogen (N) levels provide a better descriptor of tree growth. While this chapter focuses on both animal nutrition and tree growth, only CP is reported to avoid confusion. Nitrogen is an essential element for the building of amino acids and animal proteins that when available in low concentration, can affect basic physiological processes such as chlorophyll functioning and cell wall maintenance (Ferwerda 2005, Saneoka et al. 2004). (2) Acid detergent fibre provides a measure of the digestibility of the browse material (Cooper et al. 1988, Ganqa and Scogings 2007, Scogings et al. 2004). (3) Calcium, K and P are the most important (and most limiting) macro-nutrients affecting plant growth (Moore et al. 1998, Cooper et al. 1988, Ferwerda 2005). The ADF measure was chosen over neutral detergent fibre (NDF) to represent the total fibre (cell wall) concentration (Reed 1986). Total nitrogen was determined using the Dumas method (AOAC 1984), Ca, P, and K were determined according to AOAC (1984). Acid detergent fibre was determined according to Goering and van Soest (1970). Differences in leaf nutrient characteristics among species and between seasons and study areas were determined with repeated measures ANOVA (Genstat 9.1.0.147, Lawes Agricultural Trust). With repeated measurements, there is likely to be a stronger correlation between observations that are made at consecutive time points than between those that are more greatly spaced (Payne et al. 2006). To correct for this correlation, a correction factor (epsilon), as described by Greenhouse and Geisser (1959), was applied.

To investigate relations between browse production (kg/ha/quarter) and browse nutritive value, regression models were constructed using CART5.0 (Steinberg and Colla 1997). Models were developed for the whole study area for all six tree species. Explanatory variables comprised binary codes for sampling Period (1 = Jul-Sep 2003, 2 = Oct-Dec 2003, 3 = Jan-Mar 2004, 4 = Apr-Jun 2004, 5 = Jul-Sep 2004, 6 = Oct-Dec 2005, 7 = Jan-Mar 2005) and numerical values for ADF, CP, Ca, K and P (% DM). A more in-depth discussion as to the choice of non-parametric analyses is given in Chapter 3.

According to Furstenburg (2005), a low crude fibre concentration of < 40 % and a high protein concentration of > 8 % in the diet are required for proper maintenance of an impala's physical condition. Furthermore, protein content in excess of 16 % (up to 22 %) is required for growth and lactation (Furstenburg 2005). The daily food intake of impala changes seasonally from approximately 900 g DM/day in the dry season, to approximately 1900 g DM/day in the wet season (Furstenburg 2005). To determine the influence of browse nutritive value and in turn browser selection patterns on browsing capacity determinations, the daily CP (304 g (wet season) and 72 g (dry season) (g DM/day)) requirements of a 45 kg adult impala for maintenance and CP (304 g DM/day) requirements for growth, were compared with the actual browse nutrient composition of the current season's growth for each of the three study areas over eight seasons as defined in Chapter 3.

Results

Relating browse nutrient characteristics to browser selection patterns

Acid detergent fibre, C, P and K concentrations varied among plant species, within each study area, but Ca and P concentration did not (Figure 5.1). Species showed distinct groupings in their relative nutrient concentrations. Evergreen species: *C. bispinosa, E. divinorum* and *G. senegalensis*, generally not favoured (Table 3.1), were consistently not different from each other within each study areas in their ADF, CP, Ca and P concentrations, while deciduous and semi-deciduous (highly favoured species (Table 3.1)): *A. nilotica, S. africana* and *Z. mucronata* showed similar trends (Figure 5.1).

Evergreen trees, across all three study areas, had greater ADF concentrations (45-52 %) than both the deciduous (22-33 %) and semi-deciduous trees (22-26 %), although these differences were only apparent for *G. senegalensis* (across all three study areas) and for *C. bispinosa* and *E. divinorum* on MGR (Figure 5.1). By contrast, CP concentrations were greater in semi-deciduous (12-13.5 %) and deciduous (10.5-12 %) species (across all three study areas) than in evergreen species (7.5-8 %). Semi-deciduous species had the lowest ADF and the greatest CP concentrations, although these were not different to those measured in deciduous species. Calcium, K and P concentrations did not vary notably between species groupings, although the Ca and K concentrations of *Z. mucronata* were greater on MGR and PGR.

The mean nutrient concentrations (ADF, CP, Ca, K and P) of deciduous species did not vary among study areas (*P*=0.08) (Table 5.1). Semi-deciduous and evergreen species showed a similar result, except that both semi-deciduous and evergreen trees sampled on BGP had greater concentrations of phosphorus than those on MGR and PGR (*P*=0.00 and *P*=0.01 respectively) (Table 5.1).

Table 5.1: Mean nutrient concentrations (± SE) of three species guilds (Deciduous: *A. nilotica*; Semi-deciduous: *S. africana*, *Z. mucronata*; Evergreen: *C. bispinosa*, *E. divinorum*, *G. senegalensis*), studied across three study areas (BGP – Bonamanzi Game Park, MGR – Mun-Ya-Wana Private Game Reserve, PGR – Pongola Game Reserve) along the northern Zululand Coastland of KwaZulu-Natal. Letters above means indicate differences between study areas for each species guild (*P*<0.05).

Species Guild	**Mean nutrient concentration (%DM ± SE)**			**F-ratio**	***P* value**
	BGP	**MGR**	**PGR**		
<u>Deciduous:</u>					
Acid detergent fibre	33.28 ± 3.39	23.24 ± 2.67	22.02 ± 4.76	$F_{2,62}$ = 2.70	0.15
Crude protein	11.85 ± 1.01	10.46 ± 1.03	11.79 ± 2.51	$F_{2,62}$ = 0.26	0.78
Calcium	1.60 ± 0.20	0.78 ± 0.13	1.61 ± 0.41	$F_{2,62}$ = 3.95	0.08
Potassium	1.00 ± 0.12	0.76 ± 0.10	0.75 ± 0.20	$F_{2,62}$ = 0.93	0.45
Phosphorus	0.14 ± 0.02	0.10 ± 0.01	0.10 ± 0.02	$F_{2,62}$ = 1.73	0.26
<u>Semi-deciduous:</u>					
Acid detergent fibre	26.53 ± 3.26	22.01 ± 1.32	24.40 ± 3.41	$F_{2,83}$ = 2.33	0.17
Crude protein	12.22 ± 0.60	12.92 ± 0.75	13.45 ± 1.29	$F_{2,83}$ = 1.19	0.36
Calcium	1.61 ± 0.16	1.24 ± 0.08	1.31 ± 0.16	$F_{2,83}$ = 1.36	0.32
Potassium	0.86^a ± 0.07	1.39^b ± 0.09	1.24^b ± 0.14	$F_{2,83}$ = 5.68*	0.03
Phosphorus	0.19^a ± 0.04	0.11^b ± 0.01	0.13^b ± 0.01	$F_{2,83}$ = 13.90**	0.00
<u>Evergreen:</u>					
Acid detergent fibre	52.20 ± 1.52	48.53 ± 2.02	45.11 ± 2.58	$F_{2,188}$ = 1.81	0.19
Crude protein	7.64 ± 0.21	7.87 ± 0.29	8.05 ± 0.48	$F_{2,188}$ = 0.23	0.80
Calcium	1.02^a ± 0.05	0.80^b ± 0.05	1.07^a ± 0.08	$F_{2,188}$ = 6.65**	0.01
Potassium	1.01 ± 0.06	0.84 ± 0.05	1.11 ± 0.08	$F_{2,188}$ = 2.92	0.08
Phosphorus	0.12^a ± 0.00	0.09^b ± 0.01	0.10^b ± 0.01	$F_{2,188}$ = 6.71**	0.01

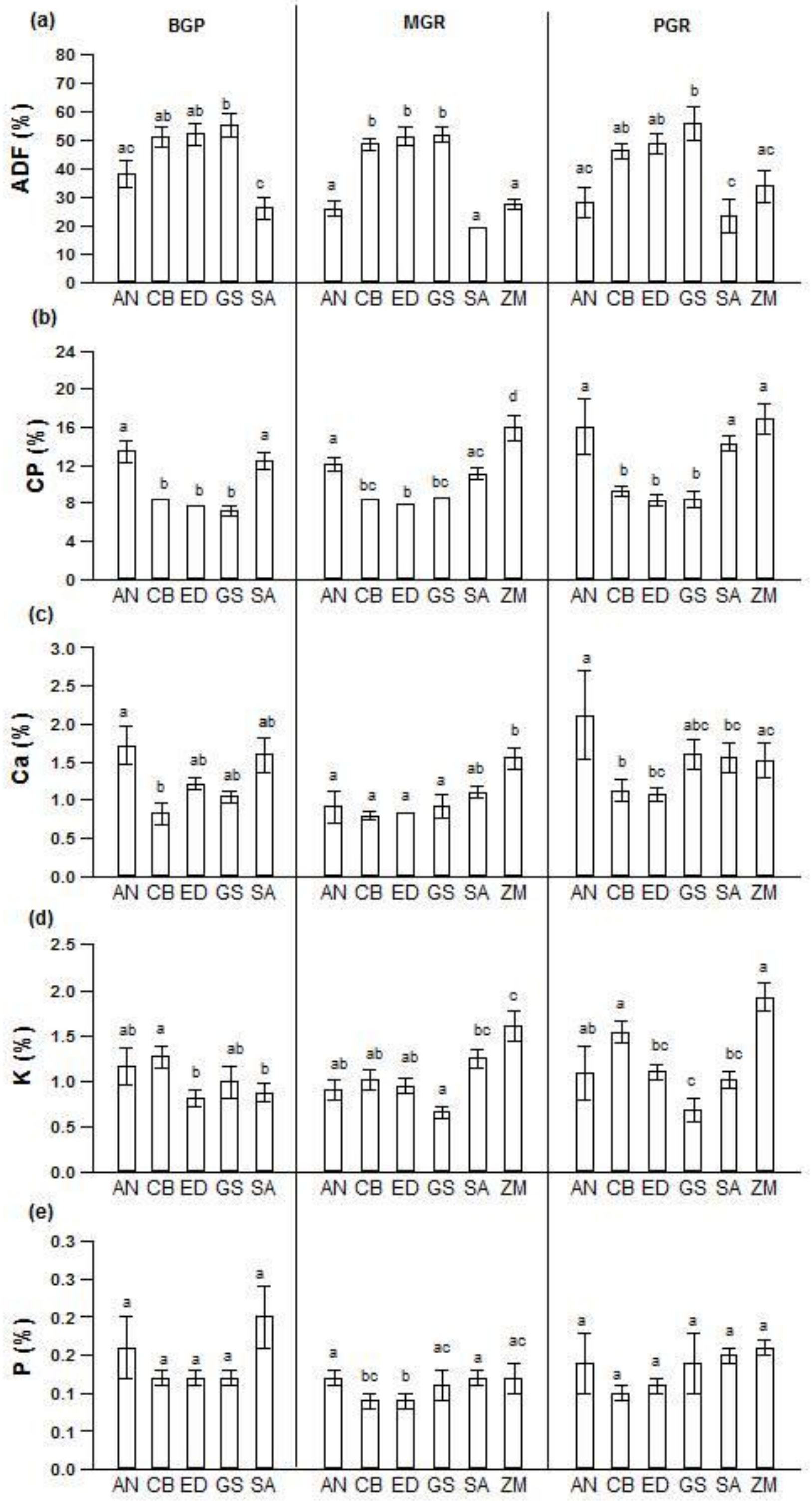


Figure 5.1: Mean (a) acid detergent fibre (ADF), (b) crude protein (CP), (c) calcium (Ca), (d) potassium (K) and (e) phosphorus (P) concentrations (%DM ± SE) of the six woody species studied over seven seasons along the northern Zululand coast, South Africa. Letters above bars indicate differences among species within each study area (BGP – Bonamanzi Game Park, MGR – Mun-Ya-Wana Private Game Reserve, PGR – Pongola Game Reserve). AN, *Acacia nilotica*; CB, *Carissa bispinosa*; ED, *Euclea divinorum*; GS, *Gymnosporia senegalensis*; SA, *Spirostachys africana*; ZM, *Ziziphus mucronata*.

Acid detergent fibre, CP, Ca, K and P concentrations varied among seasons, but the CP, K and P concentration of deciduous trees did not (Table 5.2). All three tree species guilds showed the greatest ADF concentrations at the end of the first wet season (Jan-Mar 2004) (defined in Chapter 4), and with the exception of the evergreen species, the greatest CP concentration at the end of the second wet season (Jan-Mar 2005) (Table 5.2). Acid detergent fibre and CP concentrations were generally (across all three species guilds) greater over the middle of the wet seasons into the early dry seasons, following plant growth, although these differences were not consistent. The variation in Ca, K and P concentrations across seasons showed no obvious seasonal trend, except that the greatest concentrations of K and P for deciduous and evergreen trees appeared during the first half of the first wet season (Oct-Dec 2003).

Table 5.2: Mean nutrient status (% DM ± SE) of three species guilds (Deciduous: *A. nilotica*; Semi-deciduous: *S. africana*, *Z. mucronata*; Evergreen: *C. bispinosa*, *E. divinorum*, *G. senegalensis*), studied across 7 sampling seasons along the northern Zululand Coast of KwaZulu-Natal. Letters above means indicate significant differences between seasons for each species guild (*P*<0.05). Wet season is defined as the period during the year when more than 80% of the annual precipitation falls. Dry season, conversely, is defined as the period during the year when less than 20% of the annual precipitation falls.

Species	**Mean nutrient concentration (%DM ± SE)**							**F-ratio**	**P value**
Guild	**Jul-Sep 03**	**Oct-Dec 03**	**Jan-Mar 04**	**Apr-Jun 04**	**Jul-Sep 04**	**Oct-Dec 05**	**Jan-Mar 05**		
	dry	**dry**	**wet**	**dry**	**dry**	**wet**	**wet**		
Deciduous:									
Acid detergent fibre	17.90^{a} ± 5.85	28.29^{ab} ± 4.24	40.80^{b} ± 7.48	25.53^{ab} ± 5.50	16.57^{a} ± 5.67	36.24^{b} ± 3.38	26.67^{ab} ± 1.67	$F_{2,62}$ = 3.52*	0.04
Crude protein	8.31 ± 3.10	12.54 ± 1.98	13.18 ± 1.90	9.91 ± 1.47	8.35 ± 2.87	13.44 ± 1.06	13.9 ± 0.44	$F_{2,62}$ = 1.70	0.22
Calcium	0.69^{a} ± 0.28	1.17^{b} ± 0.23	1.50^{bd} ± 0.39	2.20^{c} ± 0.51	0.55^{a} ± 0.20	1.54^{bd} ± 0.34	1.65^{d} ± 0.33	$F_{2,62}$ = 4.51*	0.02
Potassium	0.80 ± 0.33	1.25 ± 0.21	0.99 ± 0.14	0.61 ± 0.12	0.85 ± 0.29	0.84 ± 0.05	0.71 ± 0.03	$F_{2,62}$ = 1.28	0.31
Phosphorus	0.14 ± 0.06	0.15 ± 0.02	0.11 ± 0.02	0.08 ± 0.01	0.10 ± 0.04	0.12 ± 0.01	0.12 ± 0.00	$F_{2,62}$ = 0.78	0.26
Semi-deciduous:									
Acid detergent fibre	12.12^{a} ± 3.99	35.63^{b} ± 4.12	34.65^{b} ± 4.54	23.34^{c} ± 2.83	19.83^{ac} ± 1.26	20.50^{c} ± 1.04	18.84^{ac} ± 1.05	$F_{2,83}$ = 12.66**	0.00
Crude protein	5.28^{a} ± 1.61	11.98^{b} ± 1.39	13.90^{bc} ± 0.55	12.43^{bd} ± 0.46	16.04^{c} ± 1.43	14.96^{cd} ± 1.08	16.26^{c} ± 1.19	$F_{2,83}$ = 23.76**	0.00
Calcium	0.84^{a} ± 0.26	0.96^{a} ± 0.07	1.58^{b} ± 0.17	1.59^{b} ± 0.19	1.60^{b} ± 0.21	1.18^{ab} ± 0.11	1.53^{b} ± 0.12	$F_{2,83}$ = 6.84**	0.00
Potassium	0.42^{a} ± 0.13	1.30^{bc} ± 0.12	1.52^{cd} ± 0.19	1.15^{b} ± 0.12	1.36^{bc} ± 0.13	1.67^{d} ± 0.17	1.33^{bc} ± 0.16	$F_{2,83}$ = 19.32**	0.00
Phosphorus	0.05^{a} ± 0.02	0.16^{b} ± 0.01	0.13^{b} ± 0.01	0.12^{ab} ± 0.01	0.19^{b} ± 0.04	0.14^{b} ± 0.01	0.13^{b} ± 0.01	$F_{2,83}$ = 5.64*	0.04
Evergreen:									
Acid detergent fibre	40.97^{a} ± 3.00	44.57^{ac} ± 2.46	64.49^{b} ± 1.72	47.44^{acd} ± 2.84	49.09^{cd} ± 1.53	53.44^{d} ± 3.41	44.11^{ac} ± 3.36	$F_{2,188}$ = 12.11**	0.00
Crude protein	6.78^{a} ± 0.50	9.71^{b} ± 0.53	8.21^{b} ± 0.25	6.57^{a} ± 0.47	7.61^{ab} ± 0.39	8.16^{b} ± 0.41	7.82^{ab} ± 0.47	$F_{2,188}$ = 6.52**	0.00
Calcium	1.15^{a} ± 0.10	0.93^{ab} ± 0.09	0.99^{ab} ± 0.10	1.07^{a} ± 0.09	0.97^{ab} ± 0.08	0.79^{b} ± 0.06	0.88^{ab} ± 0.08	$F_{2,188}$ = 2.83*	0.05
Potassium	0.71^{a} ± 0.08	1.31^{b} ± 0.07	1.26^{bc} ± 0.11	0.66^{a} ± 0.06	1.09^{c} ± 0.10	1.03^{c} ± 0.08	0.72^{a} ± 0.06	$F_{2,188}$ = 16.66**	0.00
Phosphorus	0.08^{a} ± 0.01	0.16^{b} ± 0.01	0.12^{c} ± 0.01	0.08^{a} ± 0.01	0.12^{c} ± 0.01	0.11^{c} ± 0.01	0.08^{a} ± 0.01	$F_{2,188}$ = 30.15**	0.00

Regression tree model

Variation in browse production (kg/ha/quarter) was primarily accounted for by P (%DM) (with 7 % of the total variance for the model being accounted for) (Figure 5.3). Other important browse nutritive value factors accounting for the variation in quarterly browse production were: CP (7 %), Ca (2 %) and ADF (0.2 %), with the total model accounting for 24 % of the total variance in the dataset.

While browse nutritive value cannot directly influence the amount of browse production, the two factors are tightly linked in that with heightened production, more new growth is available that is considered more palatable i.e. a lesser ADF concentration and a greater CP and macro nutrient concentration. In general then, trees with concentrations of P greater than 0.1 % in their new leaf and shoot material had a heightened production four times that of trees with lower P concentrations. A concentration of P greater than 0.2 % yielded a further improvement in browse production by a factor of three. Trees with ADF concentrations above 55 % recorded lower production by a factor of five; trees with CP concentrations above 10 % also recorded lower production by a factor of three. Browse production was lower in trees with Ca concentrations above 1 % by a factor of 3.5.

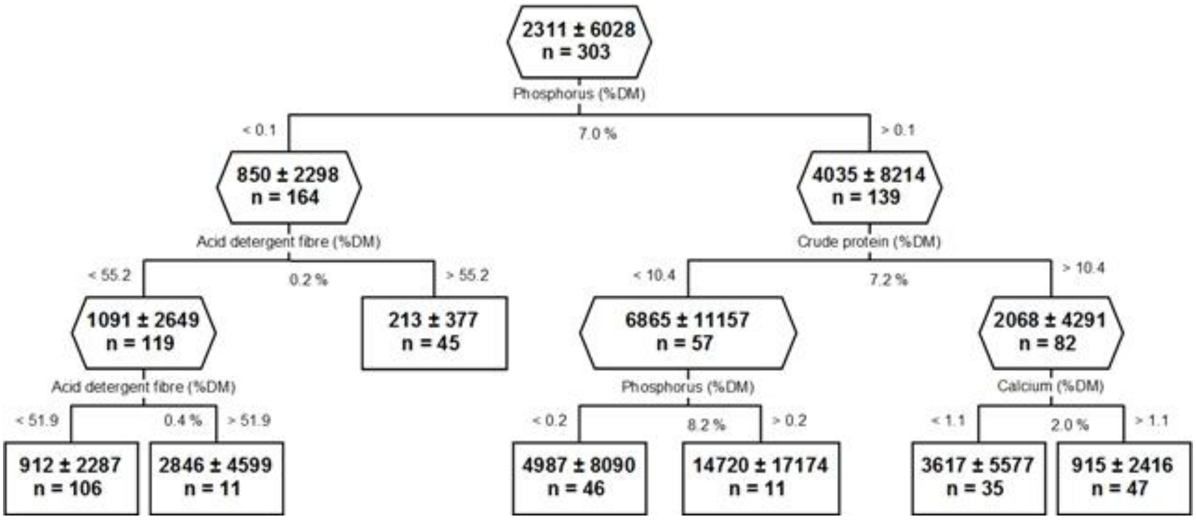


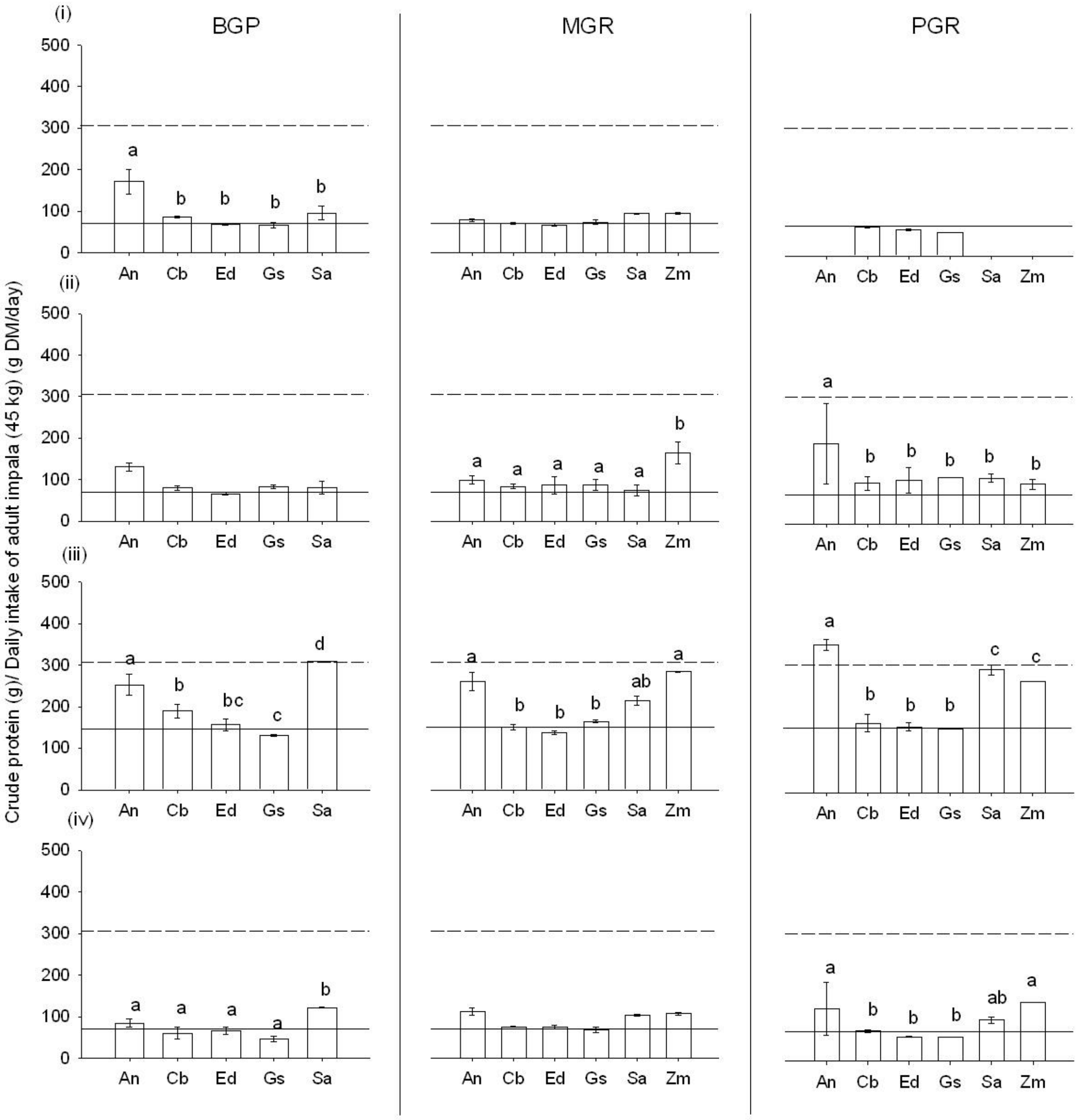
Figure 5.2: Regression tree for the browse production (kg/ha/quarter) of across three study areas, subject to various combinations of tree nutritive value characteristics (see *Data collection*). Means (±SE) for each group are presented at each dichotomy together with the splitting criterion and the percentage of the total variance accounted for by that division. Means (±SE) and the number of members of each group in the terminal (rectangle) and non-terminal (broken rectangle) leaf node are presented.

Comparisons with the daily nutrient requirements of impala

Deciduous (*A. nilotica*), semi-deciduous (*S. africana* and *Z. mucronata*) and evergreen (*C. bispinosa, E. divinorum* and *G. senegalensis*) tree species differed in their relative levels of CP required for maintenance of a 45 kg adult impala (Figure 5.3). Deciduous and semi-deciduous trees consistently contained concentrations of CP (g DM/day) above those of evergreen species. All species consistently contained concentrations of CP equal to or greater than the daily CP requirement of an adult impala (45 kg) for maintenance in both wet and dry seasons.

Differences were not measured among study areas across seasons despite differences in the MAP of the study areas (Figure 5.3). Concentrations of daily CP required for maintenance of a 45 kg adult impala for all tree species over all three study areas were greater in the wet seasons than in the dry seasons. Likewise, concentrations of daily CP required for maintenance of a 45 kg adult impala (g DM/day) for all species, over all three study areas during year 1 (Jun 2003 - Apr 2004) (below average rainfall) were significantly lower than in year 2 (Jun 2004 - Apr 2005) (above average rainfall).

During the wet seasons, daily CP requirements of an adult impala (45kg) for growth were met by *A. nilotica*, *S. africana* and *Z. mucronata* (deciduous and semi-deciduous species), and even then inconsistently over the three study areas (Figure 5.3).


(i)
BGP
MGR
PGR
500
400
300
200
100
0
a
b
b
b
b
An
Cb
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Gs
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Zm
(ii)
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(iv)
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Crude protein (g)/ Daily intake of adult impala (45 kg) (g DM/day)

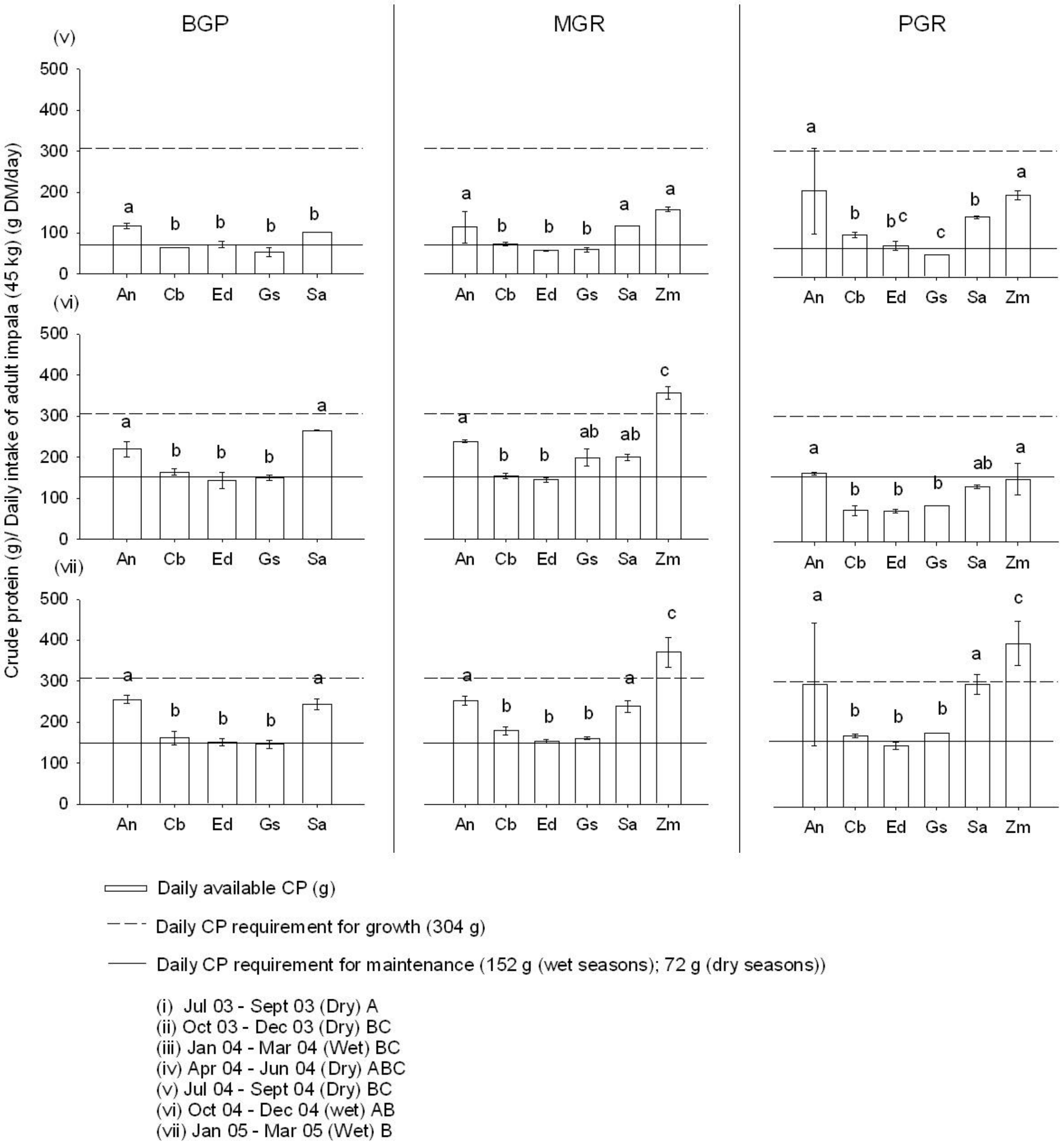

Figure 5.3: Comparison of the mean available daily crude protein (CP) (±SE) (measured at the end of each of seven sampling Periods) and recommended daily CP for growth and maintenance of a 45 kg adult impala of the six woody species studied along the northern Zululand coast, South Africa. Lower case letters above bars indicate differences (*P*<0.05) among species within each study area (BGP – Bonamanzi Game Park, MGR – Mun-Ya-Wana Private Game Reserve, PGR – Pongola Game Reserve). An, *A. nilotica*; Cb, *C. bispinosa*; Ed, *E. divinorum*; Gs, *G. senegalensis*; Sa, *S. africana*; Zm, *Z. mucronata*. Capital letters next to the roman numerals indicate differences (*P*<0.05) among seasons (over all three study areas and all six species). The absence of bar graphs for PGR (i) for species An Sa and Zm was due to insufficient browse material available on those species for sampling during that season.

Discussion

Are browse nutrient characteristics related to browser selection patterns in northern Zululand wooded savannas?

Of the tree species considered in this study, *S. africana* and *Z. mucronata* (both semi-deciduous trees) were considered to be highly favoured by browsing herbivores (Bowland 1990, Pooley 1997, Sauer et al. 1977, Rauff 2002, Tello and van Gelder 1975) while *A. nilotica* (deciduous) and *C. bispinosa* (evergreen) were considered to be favoured (Owen-Smith 1979, Owen-Smith and Cooper 1987a, Pooley 1997, Rauff 2002). *Euclea divinorum* and *G. senegalensis* (both evergreen species) were considered to be not favoured by browsing herbivores (Owen-Smith 1979, Owen-Smith and Cooper 1987a, Pooley 1997, Rauff 2002, Sauer et al. 1977).

Owen-Smith and Cooper (1987a), sought to determine the relative importance of a number of factors seen to influence browser selection patterns. These factors included: (a) nutrients and secondary metabolites; (b) physical structures, such as thorns; (c) the growth stage of the whole plant and its leaves; (d) soil nutrient and light availability and (e) previous defoliation history. Their findings led them to the conclusion that, after allowing for the effects of physical factors, such as thorns, on leaf accessibility, unpalatability must be determined by the nutrient concentrations or structural properties of the browsed material (Cooper et al. 1988). These nutrient factors can be grouped into three categories: (a) nutrients: including protein and various mineral elements; (b) fibre, including cellulose, hemicelluloses and lignin, which influence the physical toughness as well as digestibility; (c) plant secondary metabolites, which may function as toxins or to reduce the digestive availability of nutrients (Cooper et al. 1988). Considering these findings, tree species regarded as highly favoured by browsing herbivores, should in turn be those species with the most favourable nutrient concentrations, highest digestibility and lowest concentrations of plant secondary metabolites.

Crude protein and ADF concentrations among the different tree species (considered over all seven seasons) indeed confirmed these predictions, in that the highly favoured, semi-deciduous, species showed the greatest CP and lowest ADF concentrations, while species considered less palatable showed the opposite trends. While no differences were observed between favoured microphyllus species (*A. nilotica*) and favoured mesophyllus species (*S. africana* and *Z. mucronata*), a significant difference was established between evergreen species and deciduous species (of varying shades), where deciduous species showed the greatest nutrient concentrations and lowest concentrations of fibre. The difference in browser selection patterns between evergreen and deciduous species may, however, be more closely related to the differences in the secondary metabolite concentrations between the two species guilds (Cooper et al. 1988, Bergström 1992) and requires further investigation.

The next question whether study area had an effect on the nutrient composition of each species grouping (guild), i.e. can species considered highly favoured in one area, be considered unfavoured in another? The influence of study area on browse nutritive value and hence browser selection, could not be established. Acid detergent fibre and CP concentrations, within each species guild, were not different between study areas. This result might be explained by the fact that, on a large scale, rainfall and forage nutritive value are inversely related (Barnes 1979, Breman and de Wet 1983). Breman and de Wet (1983) ascribe this, in terms of grasses, to effects of different factors limiting plant growth. Crude protein concentration is greater in drier areas where water is the limiting factor, than when nutrients limit plant growth in wetter areas because of leaching. Macro-nutrients, P, K and Ca, showed no clear pattern in terms of their respective concentrations within each tree species guild between the three study areas, although differences in the P concentrations of semi-deciduous and evergreen trees, K concentrations of semi-deciduous trees and Ca concentrations of evergreen trees, between the three study areas were established. According to Owen-Smith and Cooper (1987a), soil nutrient status may be important in influencing plant defence mechanisms against vertebrate herbivory. Dominant trees and shrubs associated with infertile sandy soils have foliage that appears to be chemically defended against large herbivores. Woody plants on fertile soils, by contrast, commonly exhibit structural defences such as thorns and spines (McKey et al. 1978 cited by, Owen-Smith and Cooper 1987a, Bell 1982). Although, for giraffes, Pellew (1984a), argued that inhibitory substances are most important during periods when neither nutrient concentrations nor digestibility is limiting.

Owen-Smith and Cooper (1988) showed that certain unacceptable species become highly acceptable early in the dry season, as soon as favoured deciduous species (facultative or obligate) start shedding their leaves. Seasonal differences in browse nutritive value are important to consider, particularly in environments where the favoured species are deciduous in nature. Changes in the nutritive value of the remaining available evergreen browse, as well as the lack of new growth during the dry season will drastically affect the nutritive value and quantity of browse available to browsing herbivores and those mixed feeders which switch to browse when the grazing resource is exhausted. Season had an effect on the different nutrient concentrations of the tree species guilds studied. Acid detergent fibre levels for all tree guilds, reached a peak at the end of the first wet season in March 2004. Crude protein concentrations reached a peak in deciduous and semi-deciduous species at the end of the second wet season in April 2005, but peaked in evergreen species during the first wet season (December 2003). Likewise, concentrations of micro-nutrients were greatest during the wet seasons for all species guilds. As mammals apparently have no taste detectors for protein, the positive influence of protein on acceptability must be due to the positive association between protein levels and those of other metabolites (Cooper et al. 1988). In particular, chloroplasts account for over 50% of leaf protein (Cooper et al. 1988, Mangan and West 1977, cited by), so that high concentrations of protein are likely to result in high rates of photosynthesis, and hence in high concentrations of soluble carbohydrates (Cooper et al. 1988). Concentrations of phosphorus and potassium have also been positively correlated with protein levels. Browse nutritive value is greatest during the wet season, when growth and photosynthesis are at their highest. Further, that browse nutritive value is greatest in deciduous (varying degrees) species, which by nature exhibit faster photosynthetic rates than evergreen species (Givnish 2002). Indeed, ADF levels were lower while CP concentrations were greater during the wet seasons. Furthermore, ADF concentrations were greater and CP concentrations were lower during the first, and drier, year of sampling.

Does a relation exist between browse nutritive value and browse production?

According to Owen-Smith and Cooper (1988), there appears to be associations between plant palatability and (i) leaf chemistry, (ii) soil nutrient level, and (iii) seedling growth rate. This suggests that a relation may exist between these factors and browse production. Establishing such a relation between browse nutritive value and browse production is important for carrying capacity determinations, because if tree species with high concentrations of favourable nutrients are those species which have high production rates, then provided such species are among the dominants in any system, there should be high nutritive value food available for browsing herbivores. Browse production was positively, though somewhat weakly, correlated to concentrations of CP below 10 %, concentrations of P above 0.1 % and concentrations of Ca below 1 %. During favourable growing conditions, deciduous and semi-deciduous trees are able to maintain greater rates of photosynthesis per unit leaf mass, as a result of their greater leaf N concentration, specific leaf area, and greater intrinsic photosynthetic capacity (Givnish 2002). Since CP and P are positively related to photosynthesis, and high rates of photosynthesis are in turn related to elevated rates of growth, the relation between browse nutritive value and production is ecologically sound. These results are not supported, however, when comparing the actual production rates of the 'favoured' deciduous species with the 'unfavoured' evergreen species (Chapter 4), where the browse production of evergreen species, *E. divinorum* and *C. bispinosa*, is greater (in both wet and dry seasons) than that of deciduous and semi-deciduous species. These results are possibly a result of the differences in the tree canopy shapes and branching architecture of the different species, and relative production measures would perhaps yield different results.

Do the CP concentrations of the current season's growth of browse meet the daily nutrient requirements of impala?

Impala are recognised as a common game species throughout southern Africa, and some success has been achieved in domesticating them (Skinner et al. 1984). While impala are classified as mixed feeders, switching their diet from graze to browse in the dry season (Skinner and Smithers 1990), they often make a contribution to the browser biomass in a system, particularly on smaller properties where the numbers of larger species, like kudu and nyala are generally low. As a result they have been widely studied in terms of their food requirements (both in terms of nutrient and energy needs) and preferences. Impala, like other browsing herbivores, are highly selective in their feeding, and require a low crude fibre concentration of < 40 % and a high CP concentration of > 8 % in the diet for proper maintenance of their physical condition (Furstenburg 2005). Furthermore, CP content in excess of 16 % (up to 22 %) is required for growth and lactation (Furstenburg 2005). For the purposes of this study then, impala serve as a good species for assessing whether the current season's growth of browse met the daily nutrient requirements of browsing antelope. The daily food intake of impala changes seasonally from approximately 900 g DM / day in the dry season, to approximately 1900 g DM/day in the wet season due to the changing availability of forage (Furstenburg 2005). Should this anomaly be true for other browsing antelope, then the notion that carrying capacity determinations, based on the available biomass of forage alone, must be adjusted for resource limiting period (dry season) is unfounded, as the animals themselves adjust their intake according to the availability of food.

The daily CP requirements for maintenance for an adult impala (45 kg) were met by all species over all three study areas and all seven seasons. Daily CP requirements for growth and lactation, however, were only met by deciduous and semi-deciduous species, though this result was not consistent over study areas and years. An important consideration, in terms of protein availability, however, is that, while the CP concentration of browse is relatively high, the extent of its degradability in the rumen may be low due to the presence of interfering substances such as condensed tannins (Topps 1997).

Conclusion

The investigation of the relation between the palatability and nutritive value of savanna tree species is key in developing an understanding of what drives herbivore selection of tree species, in turn leading to the improvement of quantifying browse utilisation (resulting from herbivore selection patterns) for browsing capacity determinations. Our study sought to relate the nutrient characteristics of three tree guilds (deciduous, semi-deciduous and evergreen) to browser selection patterns. Results confirmed the prediction that highly favoured tree species (in this case semi-deciduous and deciduous species) contained the highest CP concentrations and lowest ADF levels, while species considered unfavourable showed the opposite trends. Furthermore, seasonal differences in browse nutritive value were established, with browse nutritive value being greatest during the wet season. While a relation between study area and browse nutritive value could not be established, CP concentrations for all tree guilds were highest on the driest study area, PGR.

The relation of browse nutritive value to browse production, although somewhat weak, can contribute to browsing capacity determinations. On a relative scale, tree species with the greatest concentrations of favourable nutrients are those species which have high production rates and are able to support comparatively larger numbers of browsing herbivores during the growing season when growth and lactation require improved nutrient concentrations. During the dry season, when most of the favourable tree species drop at least some of their leaves, our study showed that the nutritional requirements for maintenance of an adult impala (45 kg) are still met by the less favourable evergreen tree species.

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CHAPTER 6. PREDICTING BROWSE PRODUCTION FOR NORTHERN ZULULAND

"An experiment is a question which science poses to Nature,
and a measurement is the recording of Nature's answer."
Max Planck

Abstract

Predictive models for the production of browse on deciduous, semi-deciduous and evergreen trees in northern Zululand were developed using multivariate adaptive regression spline functions. Available canopy volume (ACVol) (m^3) was closely related to the production of browse on deciduous trees (*A. nilotica* and *D. cinerea*), with a relative variable importance of 100 %. Foliage density (FD) (0-5, measured on an ordinal scale), height to lowest leaves (HL) (m) and stem diameter (Stem D) (m) had secondary, tertiary and quaternary effects respectively on deciduous browse production with variable importance figures of 95 %, 93 % and 89 % respectively. The resulting browse production basis functions accounted for 39 % of the total variance in the data set (P=0.00). ACVol (m^3) was closely related to the production of browse on semi-deciduous trees (*S. africana* and *Z. mucronata*), with a relative variable importance of 100%. Tree height (HT) (m) and mean minimum daily temperature (MMinDT) (^oC) had secondary and tertiary effects on browse production with variable importance figures of 68 % and 41 % respectively. The resulting browse production basis functions accounted for 38% of the total variance in the data set (P=0.00). Available canopy volume (m^3) had a dominant effect on the production of browse on evergreen trees (*C. bispinosa, E. divinorum* and *G. senegalensis*), with a relative variable importance of 100%. Stem diameter (m), HL (m) and HT (m) had secondary, tertiary and quaternary effects on browse production with variable importance figures of 67 %, 32 % and 29 % respectively. The resulting browse production basis functions, accounted for 65 % of the total variance in the data set (P=0.00).

Introduction

Traditionally, stocking densities for wildlife in African savannas were set by applying the carrying capacity norms developed by agriculturalists (Meissner 1982). The term ‘carrying capacity’ is used widely but in various ways in the ecological literature (Mentis 1977, Peel et al. 1999, Caughley 1981, Dhondt 1988), and was borrowed from the agricultural sector, where it refers to domesticated grazers. The concept generally ignores browsers and the wide variety of plant types and plant parts making up browser diets (Bothma et al. 2004). Wildlife systems of southern Africa usually include grazers and browsers. Conservation of biodiversity or the production of game animals requires the effective and sustainable utilisation of the two major components of the system, the grass component and the tree component. However, the system is a complex one. The relative grazing or browsing pressure exerted by the different game animals affects the competitive balance between the herbaceous layer and the bush component, and this balance in turn affects the stocking rates for grazing and browsing animals (Stuart-Hill and Tainton 1988).

The importance of browse trees for both livestock and game production in southern Africa has long been recognised, but is possibly undervalued by the farming community (Milton 1988). In developing new and more accurate methods to determine wildlife (particularly browsing herbivores) carrying capacities for game ranching or conservation areas, it is important to have a clear understanding of what is meant by browse and available browse (Rutherford 1979). Rutherford (1979) defined browse as ‘the sum total of that material of woody species that is potentially edible to a specific set of animals, most commonly regarded as the current season’s growth of leaves and twigs’. The proportion of woody vegetation made up of potentially edible foodstuffs for herbivores (i.e. leaves and new twigs) is very low compared with grasses (Walker 1980). In addition, due to the size and morphology of woody plants, only a relatively small proportion of the leaves and twigs are considered ‘available’ to browsing ungulates. The availability of browse below a specified browse height may be further reduced by obstruction of browse material towards the centre of the plant by dense branch entanglements or thorns (Rutherford 1979), while leaf senescence of winter deciduous species will lower available browse during certain periods (Chapter 4). The utilised proportion of browse biomass is therefore generally less than 10 % (von Holdt 1999, Owen and Wiegert 1967) but can be as low as 2 % (Owen-Smith 1985). The proportion of current annual growth that is utilised, however, can be much greater (Walker 1980).

According to Aucamp (1976), browsing capacity is most influenced by the following six factors: (i) the density of the woody plants, (ii) the amount of leaf material within reach of an animal, (iii) the species composition of the woody vegetation, (iv) the palatability of woody species, (v) the digestibility of the woody species, and (vi) the growth potential of the woody species. Several methods exist to determine the density of woody plants in various woody communities (Cottam and Curtis 1956). Chapter 2 of this thesis dealt with factor (ii), the determination of available browse biomass, and Chapters 3, 4 and 5 covered the influence of different tree guilds, species palatabilities, nutritive value, and growth rates, and environmental influences on browse production and available browse biomass. While being able to describe all of these factors for a single vegetation unit or area is important in terms of browse management, and therefore game management, one aspect is still lacking, namely the ability to predict browse production and using these estimations to predict browser carrying capacities.

Our study aimed to develop further the browse production prediction models defined in Chapter 3, refining them to a tree species guild level in order to try to improve prediction accuracy.

Procedure

The rate of browse production was estimated by the quarterly measurements of the length increments of unbrowsed tagged shoots of trees protected from browsing by fenced exclosures. Browse production was estimated for seven key savanna tree species, representing three guilds: deciduous - *Acacia nilotica* and *Dichrostachys cinerea*; semi-deciduous - *Spirostachys africana* and *Ziziphus mucronata*; and evergreen - *Carissa bispinosa*, *Euclea divinorum* and *Gymnosporia senegalensis* and a range of palatability to ungulates and leaf sizes (Table 3.1).

Data analysis

Modelling using multivariate adaptive regression splines

Multivariate adaptive regression splines (MARS®), developed by Friedman (1991), is a flexible non-parametric regression method that generalizes the piecewise constant functions of classification and regression trees (CART®) to continuous functions by fitting (multivariate) splines (or base functions) in the homogenous groups (created by partitioning in CART®) and matching the values at the boundaries of these groups (Moisen and Frescino 2002). As a result, MARS® can be used in conjunction with CART®, where CART® is first used to extract the most important variables from a list of predictors, allowing MARS® to focus on the top variables from the CART® model. To date, MARS® has received little attention in the ecological fields, where it has been used primarily in the simulation of various characters relating to soil (Shepherd and Walsh 2002, Yang et al. 2004, 2003), forestry (Moisen and Frescino 2002) and precision agriculture (Turpin et al. 2003). Munoz's and Felicísimo (2004) compared statistical methods commonly used in predictive modelling, namely logistic multiple regression, principal component regression, classification and regression tree analysis and multivariate adaptive regression splines; however, MARS® and CART® achieved the best prediction success.

The seasonality of browse production was well documented in Chapters 3 and 4, with evidence that all three tree guilds experience a distinct growing season (up to 85 % of production in evergreen trees and 90 % in deciduous trees). With the assumption that browse production equates to 'utilisable' browse in carrying capacity determinations, regression models were constructed using MARS2.0 (Friedman 1991) for browse production (kg/ha/quarter) for each tree guild (deciduous, semi-deciduous and evergreen – defined in Chapter 1) only for the growing season (defined in Chapter 4) (Year 1 sampling Period 2: Oct – Dec 2003; Year 2, sampling Periods 5: Jul – Sep and 6 Oct - Dec 2004). Explanatory variables comprised binary codes for treatment (control, 'browsed') and foliage density (0-5) (ordinal scale defined in Chapter 2), and numerical values for available canopy volume (m^3) (ACVol), tree height (m) (HT), stem diameter (Stem D) (m), height of first leaves or potential leaf bearing stems (HL) (m), cumulative mean monthly rainfall for each quarter (MMR) (mm) and minimum and maximum mean daily temperature (^oC) (MinMDT and MaxMDT respectively).

Interpreting MARS® models

MARS® uses a series of linear regressions on different intervals of the independent variable ranges (i.e. subregions of the independent variable space) to attempt to approximate complex relations (Briand et al. 2004). The method is very flexible as it can adapt any functional form and is thus suitable to exploratory data analysis. A key concept in MARS® is the notion of knots, that are points that mark the end of region of data where a distinct linear regression is run, i.e., where the behaviour of the modelled function changes (Briand et al. 2004). Essentially knots delimit the intervals where different linear relations are identified for a single independent explanatory variable. In order to model the concept of knots and piece-wise linear regression splines, MARS® uses the concept of basis function.

These are functions of the form:

max(0, X-c) or
max(0, c-X)

Where X is an independent variable and c is a constant.

The role of basis functions is to re-express an independent variable X by mapping it to new variables, which are of the form described above (Briand et al. 2004). For max(0, X-c), X is set to 0 for all values of X up to some threshold value c and is equal to X for all values of X greater than c. MARS® is able to approximate any functional shape by mixing the two types of basis functions presented above and providing adequate values for c (Briand et al. 2004). In short, basis functions become the new independent variables of the resulting regression estimation models. MARS® also looks for interactions among independent variables.

MARS® ranks the independent variables included in model building according to the importance of these variables as predictors of the dependent variable. MARS® determines 'variable importance' by refitting the model after removing all terms involving the variable to be assessed and calculates the reduction in goodness of fit. All variables are then ranked according to their impact on goodness of fit. An optimal MARS® model, in terms of goodness of fit, is the one with the lowest generalized cross-validation (GCV) measure (Briand et al. 2004). The function is the MARS® prediction model based on basis functions (Briand et al. 2004). Y is the dependent variable – quarterly browse production (kg/ha) in this study – and there are N observations in the dataset. C(M) is the cost-complexity measure of a model containing M basis functions.

Equation 6.1

$$GCV(M) = \frac{1}{N}\sum_{i=1}^{N}\left[y_i - \hat{f}(x_i)\right]^2 / \left[1 - \frac{C(M)}{N}\right]^2$$

To avoid over fitting, besides the usual computation of squared prediction error, there is a cost incurred per basis function included in the model, much like adjusted R^2 in least-squares regression. In other words, C(M) is used to penalize model complexity, prevent over fitting of data, and promote the parsimony of models (Briand et al. 2004).

Results

Models for predicting deciduous browse production

Available canopy volume (m^3) had a dominant effect on the production of browse on deciduous trees (*A. nilotica* and *D. cinerea*), with a relative variable importance of 100% (Table 6.1). Foliage density (0-5), HL (m) and Stem D (m) had secondary, tertiary and quaternary effects on deciduous browse production with variable importance figures of 95 %, 93 % and 89 % respectively (Table 6.1). The resulting browse production basis functions, accounted for 39 % of the total variance in the data set ($P<0.001$) (Table 6.2).

Table 6.1: Relative variable importance for deciduous growing season model of browse production (kg/ha/quarter). Piecewise cubic fit on four basis function, GCV = 8353330.00 (loss in GCVOL is denoted as '-gcv').

Variable	Importance	-gCV
Available canopy volume (m^3)	100.00	9503490.00
Foliage density (0-5)	95.29	9393670.00
Height to lowest leaves (m)	93.11	9344570.00
Stem diameter (m)	89.28	9261060.00

Table 6.2: Ordinary least squares results for deciduous growing season model of browse production (kg/ha/quarter).

N: 72 **Adjusted R^2: 0.39**

Parameter	Estimate	S.E.	T-Ratio	P-Value
Constant	-267.80	487.47	-0.55	0.58
Basis Function 1	-1282.61	338.60	-3.79	0.00
Basis Function 2	8830.85	2430.54	3.63	0.00
Basis Function 3	74.42	19.02	3.91	0.00
Basis Function 4	4149.27	1111.96	3.73	0.00

$F_{4,67} = 12.49$; $P<0.00$ **S.E. of Regression = 2573.05**

Equation 6.2: Basis Functions for the deciduous growing season browse production (kg/ha/quarter) MARS® model.

BF1 = max(0, 3 - Foliage density (0-5));
BF2 = max(0, Stem diameter (m) - 1.08);
BF3 = max(0, Available canopy volume (m^3) - 0.02);
BF4 = max(0, 1.11 - Height to lowest leaves (m));

Y = -267.80 - 1282.61(BF1) + 8830.85(BF2) + 74.42(BF3) + 4149.27(BF4)

Browse production in semi-deciduous trees remained unaffected by low foliage densities but rapidly increased at foliage densities above 0.5 (Figure 6.1a). At FDs above 3.0, quarterly browse production (kg/ha/quarter) remains constant (Figure 6.1a), producing three linear regression splines and one basis function (Equation 6.2, BF1) to describe the relation between browse production and foliage density.

Browse production increased at a constant rate with increases in Stem D above 1.08 m (i.e. two linear regression splines and one basis function (Equation 6.2, BF2) developed) (Figure 6.1b).

Browse production increases at a constant rate between ACVols of the range 0.02 – 73.47 m^3 (Figure 6.1c). The resultant response of browse production to ACVol is in the form of one linear regression spline and one basis function (Equation 6.2, BF3).

Browse production is at its greatest when the HL was at its lowest (0.2 m), decreasing at a constant rate with increases in the height to the lowest leaves below 1.11 m, beyond which browse production remained negligible (Figure 6.1d). The resultant response of browse production to HL is in the form of two linear regression splines and one basis function (Equation 6.2, BF4).

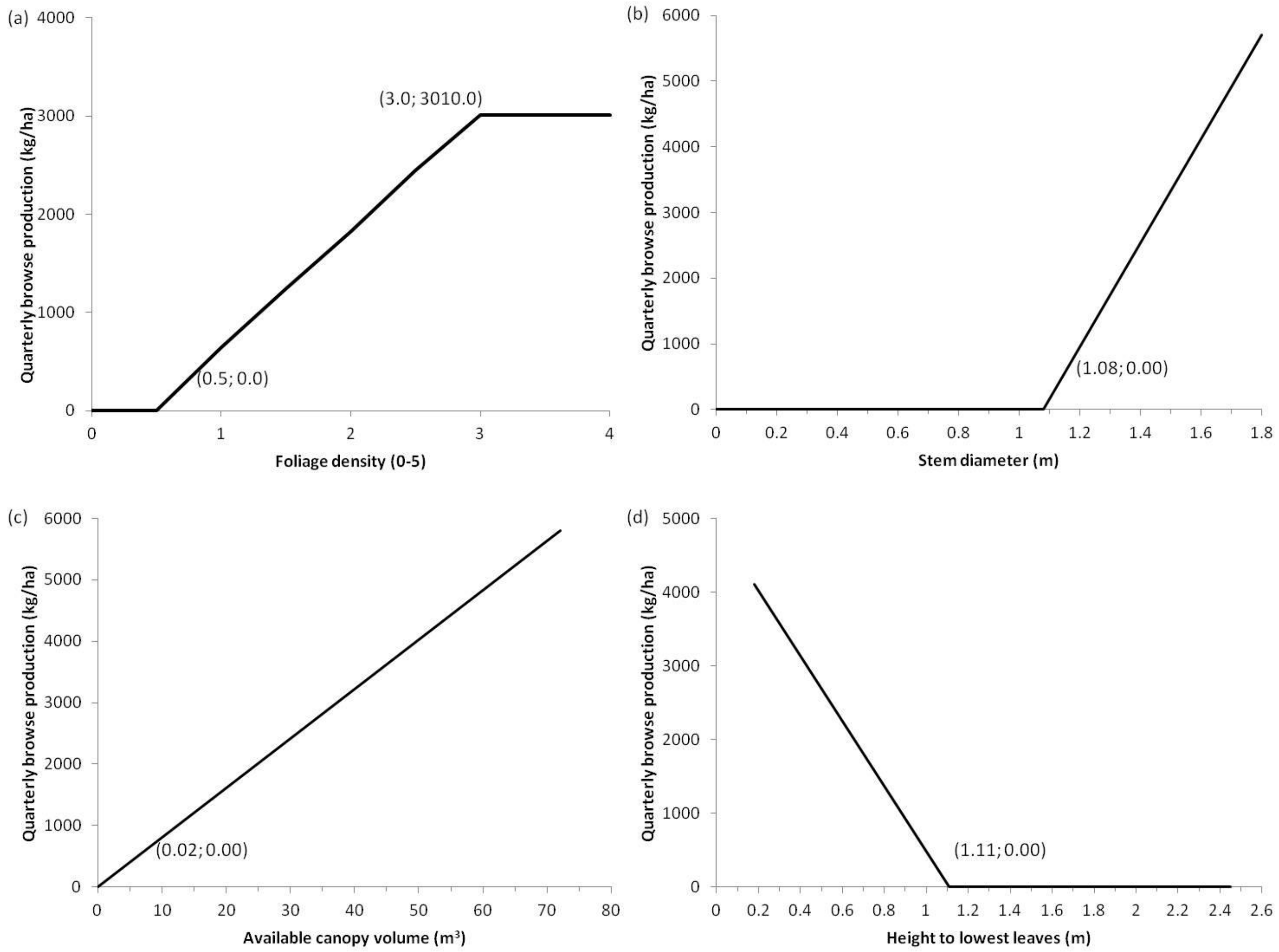

Figure 6.1: The relation between (a) foliage density, (b) stem diameter, (c) available canopy volume and (d) height to lowest leaves and quarterly browse production in deciduous trees (*Acacia nilotica* and *Dichrostachys cinerea*) (Pure ordinal contribution).

Models for predicting semi-deciduous browse production

Available canopy volume (m^3) had a dominant effect on the production of browse on semi-deciduous trees (*S. africana* and *Z. mucronata*), with a relative variable importance of 100 % (Table 6.3). Tree height (m) and MMinDT (^{o}C) had secondary and tertiary effects on browse production with variable importance figures of 68 % and 41 % respectively (Table 6.3). The resulting browse production basis functions, accounted for 38 % of the total variance in the data set ($P<0.001$) (Table 6.4).

Table 6.3: Relative variable importance for semi-deciduous growing season model of browse production (kg/ha/quarter). Piecewise cubic fit on three basis function, GCV = 38467300.00 (loss in GCV is denoted as '-gcv').

Variable	Importance	-gcv
Available canopy volume (m^3)	100.00	45383500.00
Tree height (m)	68.17	39915100.00
Mean minimum daily temperature (^{o}C)	40.84	36872300.00

Table 6.4: Ordinary least squares results for semi-deciduous growing season model of browse production (kg/ha/quarter).

N: 50 **Adjusted R^2: 0.38**

Parameter	Estimate	S.E.	T-Ratio	P-Value
Constant	-4522.71	1675.21	-2.67	0.01
Basis Function 1	-7943.89	2230.18	-3.56	0.00
Basis Function 2	477.74	104.93	4.55	0.00
Basis Function 3	932.72	325.44	2.87	0.02

$F_{3,46} = 11.06$; $P<0.00$ **S.E. of Regression = 5131.71**

Equation 6.3: Basis Functions for the semi-deciduous growing season browse production (kg/ha/quarter) MARS® model.

BF1 = max(0, Tree height (m) - 5.78);
BF2 = max(0, Available canopy volume (m^3) - 0.77);
BF3 = max(0, Mean minimum monthly temperature (^{o}C) - 13.11);

Y = -4522.71 - 7943.89(BF1) + 477.74(BF2) + 932.72(BF3)

Browse production remained constant at HT below 5.78 m, thereafter it decreased at a constant rate, producing two linear regression splines and one basis function (Equation 6.3, BF1)

Browse production increased at a constant rate between ACVol of the range 0.77 – 45.83 m^3 (Figure 6.2b). The resultant response of browse production to ACVol is in the form of one linear regression spline and one basis function (Equation 6.3, BF2).

Browse production increased at a constant rate at MMinDT above 13.11 ^{o}C (Figure 6.2c). The resultant response of browse production to MMinDT is in the form of one linear regression spline and one basis function (Equation 6.3, BF3).

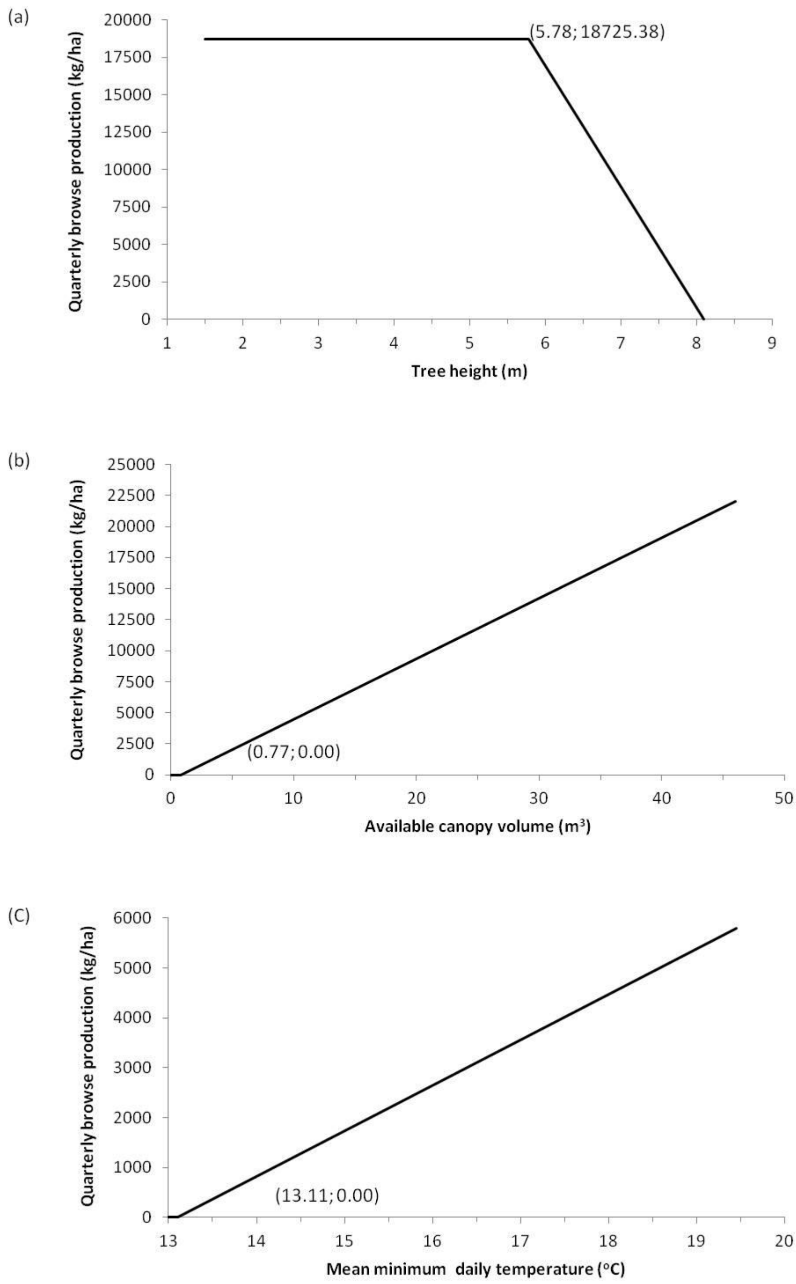

Figure 6.2: The relation between (a) tree height, (b) available canopy volume and (c) mean minimum daily temperature and quarterly browse production in semi-deciduous trees (*Spirostachys africana* and *Ziziphus mucronata*) (Pure ordinal contribution).

Models for predicting evergreen browse production

Available canopy volume (m^3) had a dominant effect on the production of browse on evergreen trees (*C. bispinosa, E. divinorum* and *G. senegalensis*), with a relative variable importance of 100 % (Table 6.5). Stem diameter (m), HL (m) and HT (m) had secondary, tertiary and quaternary effects on browse production with variable importance figures of 67 %, 32 % and 29 % respectively (Table 6.5). The resulting browse production basis functions, accounted for 65 % of the total variance in the data set ($P<0.001$) (Table 6.6).

Table 6.5: Relative variable importance for evergreen growing season model of browse production (kg/ha/quarter). Piecewise cubic fit on 4 basis function, GCV = 34600700.00 (loss in GCV is denoted as '-gcv').

Variable	Importance	-gcv
Available canopy volume (m^3)	100.00	51630700.00
Stem diameter (m)	66.94	39741100.00
Height to lowest leaves (m)	32.45	32355300.00
Tree height (m)	29.33	31939300.00

Table 6.6: Ordinary least squares results for evergreen growing season model of browse production (kg/ha/quarter).

N: 50 **Adjusted R^2: 0.65**

Parameter	Estimate	S.E.	T-Ratio	P-Value
Constant	193.80	684.53	0.28	0.78
Basis Function 1	-12133.17	1981.69	-6.12	0.00
Basis Function 2	-6746.99	1991.51	-3.39	0.00
Basis Function 3	38065.21	10612.91	3.59	0.00
Basis Function 4	1648.58	187.72	8.78	0.00

$F_{4,95}$ = 46.00; *P*=0.00 **S.E. of Regression = 5018.82**

Equation 6.4: Basis Functions for the evergreen growing season browse production (kg/ha/quarter) MARS® model.

BF1 = max(0, Stem diameter (m) - 0.83);

BF2 = max(0, Tree height (m) - 3.07);

BF3 = max(0, 0.11 - Height to lowest leaves (m));

BF4 = max(0, Available canopy volume (m3) - 5.52);

$$Y = 193.80 - 12133.17(BF1) - 6746.99(BF2) + 38065.21(BF3) + 1648.58(BF4)$$

Browse production in evergreen trees exhibited an inverse relation to Stem D, with production remaining high at Stem Ds below 0.83 m, but decreasing at a constant rate thereafter (Figure 6.3a). The resultant response of browse production to Stem D is in the form of two linear regression splines and one basis function (Equation 6.4, BF1).

Browse production remained constant at HTs below 3.07 m, thereafter it decreased at a constant rate (Figure 6.3b), producing two linear regression splines and one basis function (Equation 6.4, BF2).

Browse production is at its greatest when the HL was at its lowest (0.1 m), decreasing at a constant rate with increases in HL below 0.11 m, beyond which browse production remained negligible (Figure 6.3c). The resultant response of browse production to HL is in the form of two linear regression splines and one basis function (Equation 6.4, BF3).

Browse production increased at a constant rate between ACVols of the range 5.52– 41.68 m^3 (Figure 6.3d). The resultant response of browse production to ACVol is in the form of two linear regression splines and one basis function (Equation 6.4, BF4).

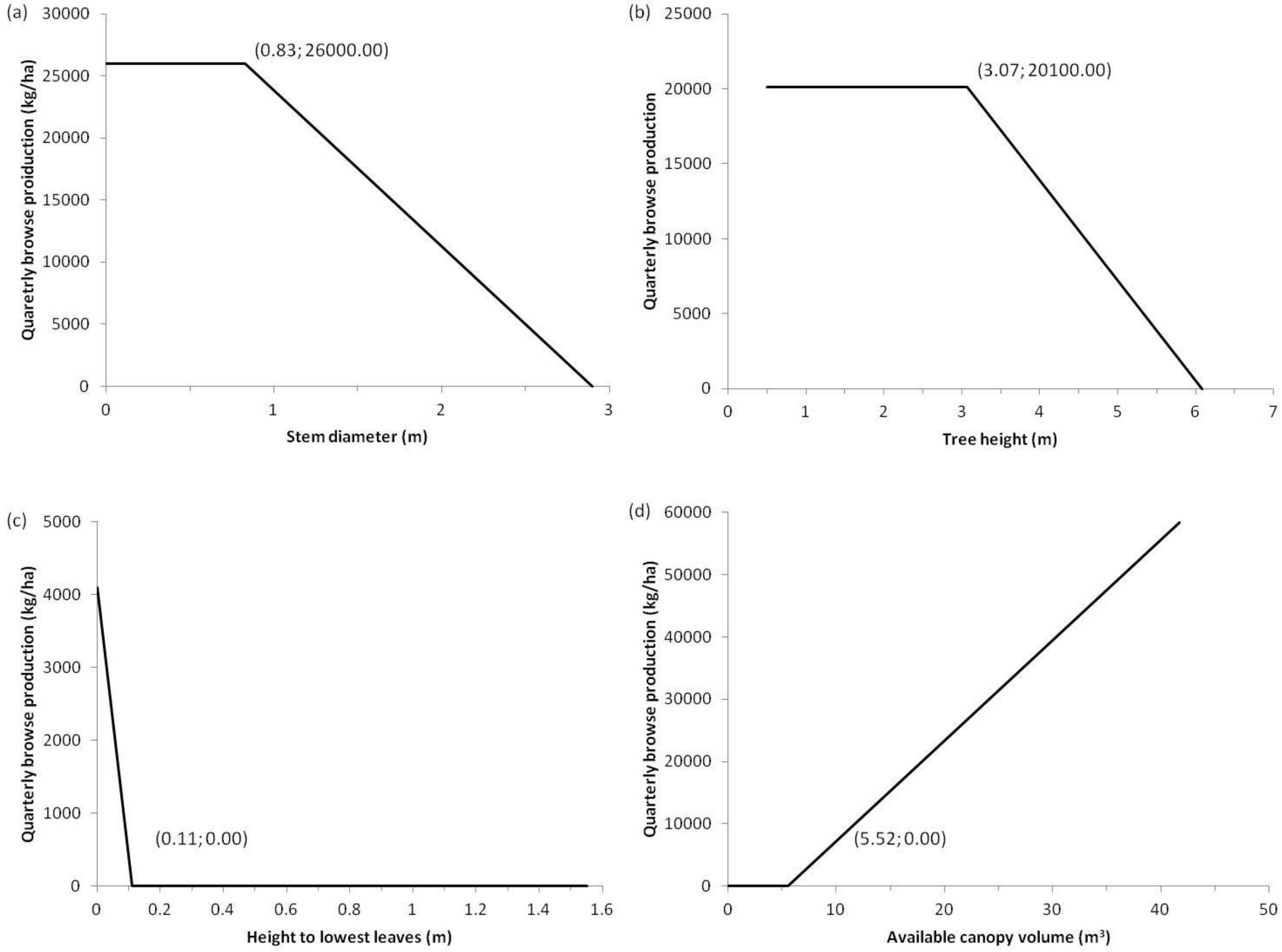

Figure 6.3: The relation between (a) stem diameter, (b) tree height, (c) height to lowest leaves and (d) canopy volume and quarterly browse production in evergreen trees (*Carissa bispinosa, Euclea divinorum* and *Gymnosporia senegalensis*) (Pure ordinal contribution).

Discussion

The determination of browser carrying capacity for conservation or ranching systems requires quantitative data on the capacity of the browse resource to support browsers (Bothma et al. 2004). The highly selective nature of browsing herbivore foraging of plant species and plant parts has received much attention (Pellew 1984a, Breebaart 2000, van der Waal and Smit 2003, Illius and Gordon 1993, Kotze and Zacharias 1993, Owen-Smith and Cooper 1983, 1987a, Cooper et al. 1988, Owen-Smith and Cooper 1989, Owen-Smith and Cooper 1988). The amount of available browse that is actually utilised by browsing herbivores is difficult to determine (Pellew 1981, Bergström 1992), although estimates range from 2 - 18% (Owen and Wiegert 1967, von Holdt 1999, Owen-Smith 1985, Goodman 1975) of the standing browse biomass. Determinations of browser carrying capacity need therefore, to be based on utilisable browse biomass rather than on available browse biomass. Our study indicated that during the growing season, browsing herbivore utilisation (in terms of plant part) is generally limited to new, more palatable, growth – i.e. browse production. The prediction and measurement of browse production, therefore, allows for the more accurate determination of browser carrying capacity and monitoring of the woody component of semi-arid savannas.

Determinants of tree size and shape, although governed by inherited developmental tendency, are largely related to the prevailing environment (Givnish 2002, Novoplansky 2003, Arzai and Aliyu 2010). The size of a tree canopy and its height above ground determines the total amount of light that the tree will intercept for photosynthesis (Arzai and Aliyu 2010). The use of measurable tree dimensions for the prediction and measurement of browse production is therefore feasible. Tree dimensions are also much quicker, cheaper and easier to measure than their environmental determinants, and find a greater application at the reserve management level.

The measureable tree dimensions identified as predictors in the MARS® models were similar for all of the tree guilds. Available canopy volume was identified as the most important predictor variable in the deciduous, semi-deciduous and evergreen browse production MARS® models. Chapter 3 highlighted the importance of this factor in the determination of browse production and argued that canopy size (defined by the number of branches) would define the number of potential sites for growth (branch tips).

Several studies have reported stem diameter being highly correlated with leaf dry mass (e.g. Rutherford 1979, Schuster 1965). Whilst stem diameter was discarded as a measure of browse available biomass (reasons given in Chapter 2), this may largely be attributed to the calculation of browse biomasses during the dormant season, when deciduous trees support few leaves. Since browse production predictions are based on the growing season flush, the use of stem diameter as a predictor may be feasible. Based on the argument that all the nutrients and water required in leaf and browse production, maintenance and growth have to pass through the plant stem, and since true deciduous trees have to replace their entire canopy during the growing season, it is intuitive that a positive relation should exist between stem diameter and deciduous browse production. It is important to note that production, as measured here, is based on the increments in shoot length and not on total leaf production. *Acacia* spp. produce leaves on old wood before shoots extend (Milton 1987). Milton (1988) hypothesizes, therefore, that twig growth in *A. tortilis* is a product of current rather than stored photosynthates. Since growing season leaf biomass or leaf flush may be predicted from stem diameter, and leaf flush determines the rate and net accumulation of photosynthates which drive browse production, the relation between browse production and stem diameter for deciduous trees is realistic.

In deciduous trees there is a lag phase in production at low levels of foliage density, where at low foliage densities, much of the stored carbohydrates are invested in producing new leaves on old woody stems, leaving fewer reserves for production. Once a full canopy is attained, at higher foliage densities, the photosynthetic rates of the leaves themselves drive subsequent browse production, as with deciduous trees.

Semi-deciduous and evergreen production is seen to remain at a constant rate with increasing tree height, up until a point, beyond which production rates steadily decline. It seems that tall trees invest more energy in maintaining their leaf biomass, than in growth. This seems feasible in that very large trees seldom have to compete for light. They are large as a function of their competitive ability to grow tall and wide and out-compete other trees around them, and have reached the limits of their ability to grow larger, based on the current prevailing environmental conditions. Growth is therefore limited mainly to the production of new leaves and the replacement of old, dead branches.

The relation between the height to the lowest leaves of the tree canopy and browse production in semi-deciduous and evergreen trees is the inverse of that for maximum tree height, with production remaining high at shorter lowest leaves heights and decreasing as the canopy is lifted higher off of the ground. This response is largely due to the phenology of the study trees involved. *C. bispinosa*, *E. divinorum* and *Z. mucronata* tend to be multi-stemmed, much branched trees with rounded canopies that often ‘sweep’ ground level (Pooley 1997).

Semi-deciduous species, more so than either of their counterparts, are the most dynamic in terms of their ability to track environmental changes. The degree of deciduousness has been related to the level of the water table (Do et al. 2005), the soil nutrient content and available soil moisture (Chapters 1,3 and 4) and to mean minimum daily temperature (Figure 6.2c) (Chidumayo 2001). Semi-deciduous species therefore have the potential to swing between a true deciduous state (under unfavourable conditions) and a true evergreen state (under favourable conditions). It is intuitive, therefore, that the best predictors of semi-deciduous browse production are measures of the prevailing climatic conditions. The influence of temperature on semi deciduous browse production, however, cannot be considered separately to the influence of rainfall. The start of shoot growth in savanna trees occurs during the dry season, 1-3 months before the start of the rainy season (Teague 1989). In his study of the relation between tree shoot extension and climate, Chidumayo (2001) showed that minimum temperature (of the range 12.4-17.5 ^{o}C) accounted for the largest variation in average monthly shoot extension in *Brachystegia boehmii, Julbernardia globiflora* and *Acacia polyacantha*. The interaction between annual rainfall and minimum temperature further accounted for the largest variation in shoot extension rate in *B. boehmii, J. globiflora* and *A. polyacantha (Chidumayo 2001)*.

While the various predictors for the production of browse in deciduous, semi-deciduous and evergreen trees make ecological sense, are relatively easy to measure and the resulting prediction models are all significant (P<0.001), the adjusted R^2 values for the models remain between 38-65%. The present study clearly illustrates certain limitations of the current approach in providing an adequate understanding of browse production in tropical savannas. The role of climatic determinants is based purely on prevailing climatic conditions at the time of the study, with northern Zululand experiencing, during the study, lower than average annual rainfall in 2003 and 2005 (up to 40% below MAR). Chapter 4 identified large differences in the browse production of the same species on the different study areas along the northern Zululand coast. Our browse production prediction models, however, necessitated the grouping of study areas for each tree guild to achieve acceptable degrees of freedom for parsimonious model building.

Conclusion

The prediction of growing season browse production is possible using measurable plant dimensions. A trade-off exists between building individual species models with improved accuracy and building general models (species groups) with wider application potential. Game conservation and ranching areas require a browse management tool that has a general application, is easy and quick to apply and can be used by non-scientists. The models presented in this chapter provide a means of not only predicting growing season browse production, but also assisting in the monitoring of the browse component by comparisons of production estimates over time. The large inherent variability in browse production measurements, even within concentrated growing season and species groupings, still remains and accounts for the reduced r^2 values of the deciduous and semi-deciduous models in particular. Further stratification of browse production measurements into key game feeding levels, tree height, or canopy volume groups may assist in building more robust models.

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CHAPTER 7. BROWSE QUANTITY AND NUTRITIVE VALUE IN THE CONTEXT OF CARRYING CAPACITY DETERMINATIONS: A SYNTHESIS

“The scientist is not a person who gives the right answers,
he's one who asks the right questions.”
Claude Lévi-Strauss

Introduction

The maintenance of large wild herbivores in discrete conservation areas poses management challenges. Boundary fences limit dispersion and migration, forcing animals to forage continuously in a limited array of vegetation communities, increasing the risk of range deterioration. The artificial confinement of herbivores characteristic of most southern African wildlife reserves is regarded as being one of the main justifications for culling. The gamut of agricultural experience in South Africa has shown that veld cannot withstand heavy continuous grazing. Before the arrival of European settlers, the wild herbivores probably occurred at high densities at a given locality only temporally. Today they are confined, and display similar area and species selection to domestic animals. This selective grazing is acute particularly in regions like KwaZulu-Natal that have an extreme heterogeneity of soils, terrain, variable annual rainfall and veld types. The concept of selective browsing and the possible effects this would have on the woody component of savanna ecosystems is yet to be fully investigated, although du Toit *et al.* (1990) suggest that severe selective browsing may lead to the replacement of more palatable species by less palatable and productive species. The developing understanding of plant-herbivore relationships indicates that natural veld provides food in abundance for the large bulk and roughage eaters. Cattle are large bulk and roughage eaters, and by virtue of the ease with which they are manipulated, can be stocked at high and variable densities, provided management is of a high standard. Concentrated food resources, upon which browsing ungulates depend, however, are generally scarce.

Ecosystem functioning in African savannas has been described as highly plastic and complex and these environments are heterogeneous in nature. Under such conditions it might be argued that conventional concepts of carrying capacity (defined by Caughley (1981)), as a descriptor of the actual/real potential for a particular plant community or mixture of communities to support a particular variety and number of large herbivores, is overly simplistic. Indeed, on a single property, carrying capacities may vary for different times of the year, from year to year and on different parts of the property. Ultimately due to the selective feeding behaviour of many wild ungulates, particularly browsing species, some areas will remain under-utilised and others over-utilised.

Broad-scale determinants of African browser carrying capacity (Figure 7.2)

When attempting to set wildlife stocking densities for conservation or ranching systems, especially for a diversity of grazers and browsers of different sizes, traditional methods of determining carrying capacities are vague and somewhat unsatisfactory. Setting stocking densities for wild herbivores requires quantitative data on the capacity of the plant resources to support herbivores (Bothma et al. 2004). Models have been described whereby the available quantity and to a lesser extent, nutritive value of browse (Chapters 2,3,4 and 5, Barnes et al. 1976, Rutherford 1979, Teague et al. 1981, Smit 1996) of each plant community on a given ranch or nature reserve can be calculated by using information from appropriate plant ecological surveys. For determining the grazing capacity of a system, available graze biomass, as well as grass species palatabilities, are sufficient because grazers are generally less selective in their foraging, in terms of plant parts, plant species, and to a certain extent (in the case of bulk feeders) plant age. Browsing herbivores on the other hand are generally highly selective feeders, utilising a small percentage of the available browse biomass (up to 10%) (Owen and Wiegert 1967, von Holdt 1999), selecting for new shoots, and young plant material. Determinations of browser carrying capacity, based on available browse biomass estimates are therefore greatly inflated. It was for this reason that our study was initiated; with the aim of modelling browse production rates of different key savanna tree species in the northern Zululand region of KwaZulu-Natal, with the assumption that browse production equates to utilisable browse biomass.

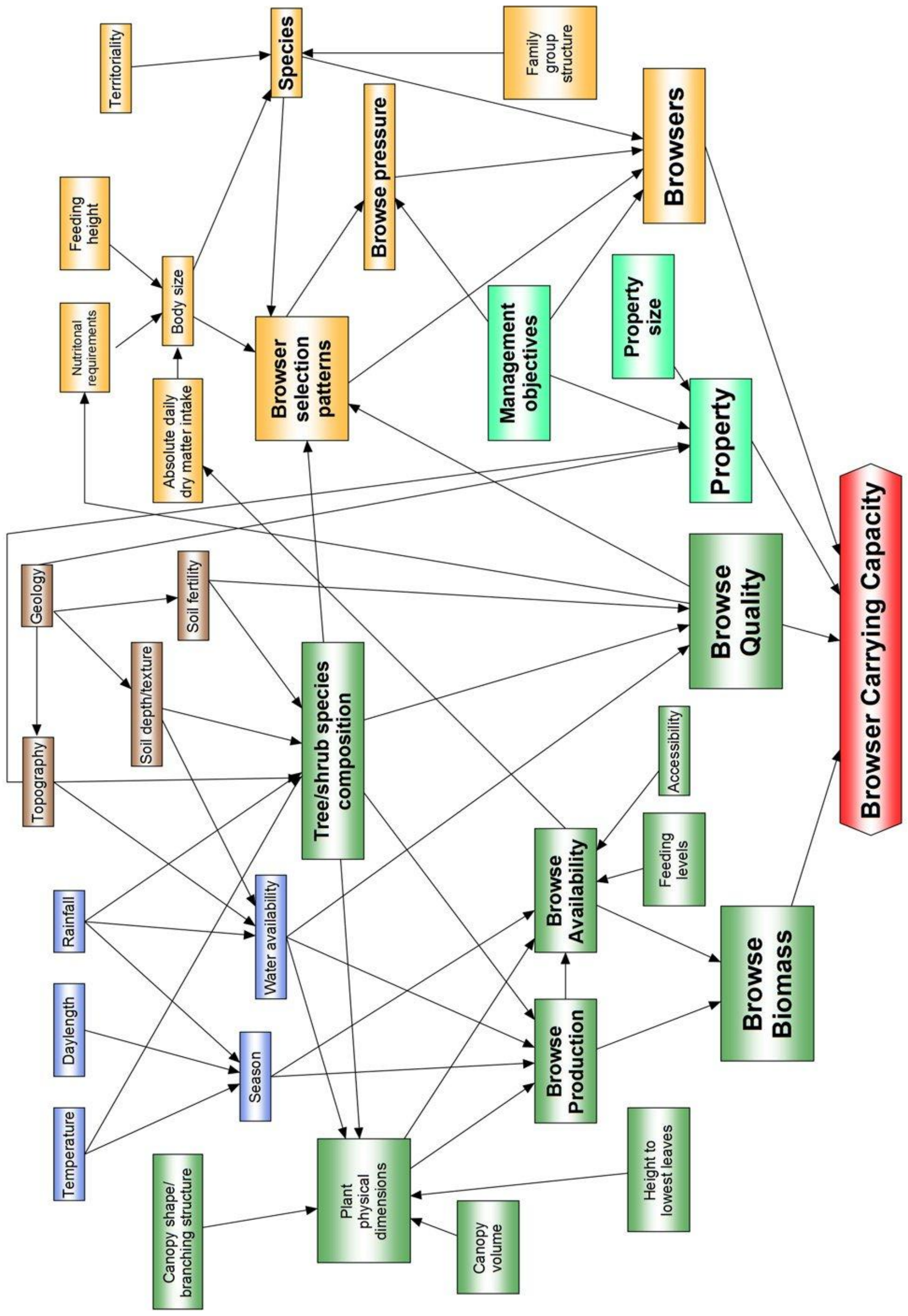

Figure 7.1: A summary of the relations between the broad scale determinants of African browser carrying capacity (as discussed above).

Browse availability

Most current methods of browser capacity determination employ some measure of available browse (Bezuidenhout 2005, Mentis and Duke 1976, Stuart-Hill and Aucamp 1993, Dhondt 1988, Rowe-Rowe and Scotcher 1986, Fritz and Duncan 1994, Furstenburg 2002, Petrides 1975, Phillipson 1975, Adcock 2001, Mentis 1977, Bothma et al. 2004). A comparison of leaf dry mass (g dry matter) (LDM) per unit canopy volume (ln m^3) (CVol) between microphyllus, deciduous (*A. nilotica*), mesophyllus, semi-deciduous (*S. africana*) and macrophyllus, evergreen (*E. divinorum* and *G. senegalensis*) trees (Figure 7.2), indicates trees with macrophyllous leaves have a proportionately greater browse biomass than both microphyllus and mesophyllus trees. Since these regression relations were derived during the dry or dormant season (Chapter 2), and since most microphyllus and some mesophyllus trees are deciduous, this result is expected. The vast structural differences in the canopy size, depth and arrangement between evergreen macrophyllus trees, such as *E. divinorum* and flat-crown, umbrella shaped canopies of *Acacias* also accounts for the differences in the potential biomass that each guild is able to support, in the form of leaves, twigs and shoots. Another consideration is the differences in the structural support in the leaves of the different guilds. Due to the disposable nature of microphyllus or deciduous leaves, less investment is placed in structural support, in the form of fibres, cellulose etc., or in herbivore defences (Givnish 2002). By their very nature, therefore, microphyllus leaves (a single compound leaf made up of a number of leaflets) weigh less than their macrophyllous counterparts of equal size.

Mesophyllus trees support a lower browse biomass at larger CVols, than do microphyllous trees. Since these relations were developed based on *S. africana* (mesophyllus) and *A. nilotica* (microphyllus) it is important to consider the structural differences between these two species in order to explain this result. Both species are much branched, with dense canopies in older, larger trees (Pooley 1997). Leaf production is greater in *A. nilotica* however, with three to four leaves clustered at each node, compared to the alternate leaf arrangement of *S. africana* (Pooley 1997). Because browse biomass, in our study, is measured by leaf dry mass, this result was expected.

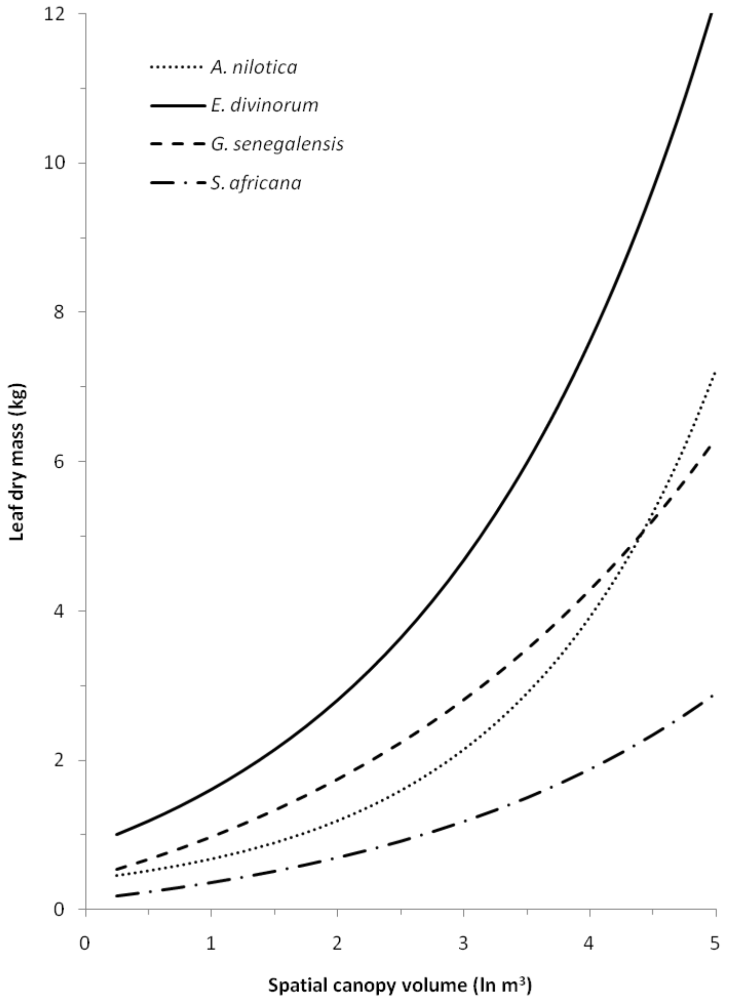

Figure 7.2: Comparison of the regression analyses of the relation between canopy volume (normal logarithm conversion) (independent variable) and leaf dry mass (dependent variable) for microphyllus (*Acacia nilotica*), mesophyllus (*Spirostachys africana*) and macrophyllus (*Euclea divinorum* and *Gymnosporia* senegalensis) trees, as determined by Chapter 2.

Browse production determinants

Species

The woody plant species in the study areas varied in their phenology, creating three major subdivisions, namely deciduous, semi-deciduous and evergreen species (Chapter 4). The deciduous trees *A. nilotica* and *D. cinerea*, grow more rapidly over a shorter growing season and are successful in competitive situations (Milton 1987, Teague 1988a, Cresswell et al. 1982). These species generally show high potential growth rates, and have the ability to grow quickly when conditions are favourable (van Essen et al. 2002). The deciduous species rely on deep rooting and usually have palatable, small and compound leaves (Coley 1983). While relative rates of browse production are higher in deciduous species, however, by the very nature of their deciduousness, absolute browse production rates are lower than their semi-deciduous and evergreen counterparts.

The evergreen trees *C. bispinosa, E. divinorum* and *G. senegalensis* are more specialized in coping with dry conditions, relying on deep rooting and secondary thickening of their leaves to be able to tolerate desiccation (van Essen et al. 2002). In comparison with deciduous and semi-deciduous species, evergreen species have moderate growth rates, are generally larger trees, and have a lower digestibility, making them less palatable to browsing herbivores (Coley 1983). Although evergreen species have a lower relative production rate than their deciduous counter-parts, due to their larger size, bigger canopies and greater leaf mass, their absolute browse production is greater and more constant across the year. While evergreen trees are generally considered less palatable, some species are highly selected by game animals, e.g. *C. bispinosa*. Evergreen trees also provide an important resource during the dry season, when many deciduous trees lose their leaves, and many grasses become dormant. The prediction of evergreen species production, particularly during the dry season, is therefore important in terms of any kind of wildlife management.

Comparing browse production as a percentage of browse biomass gives a more accurate idea of the relative production rates of the different tree guilds (Table 7.1). It was expected that browse production would be greater in species exhibiting some form of deciduousness than evergreen species. This result was confirmed for semi-deciduous *S. africana* but not for deciduous *A. nilotica.* The reasoning behind this prediction is that evergreen species have to continually invest energy into the maintenance of leaves, year round, and thus any growth or browse production is supported by concurrent photosynthesis alone (Teague 1988b). Deciduous species, due to their dormant nature during the dry season, are able to conserve energy, allowing the production of browse to be supported by a larger base of stored photosynthates. Deciduous species respond more rapidly to favourable growing conditions and with more vigour than evergreen species (Rooke et al. 2004).

Table 7.1: Mean growing and non-growing season browse production (kg/ha/quarter ± SE) as a percentage of browse biomass (LDM (kg)) for each species guild (determined using the non-linear regression equations developed in Chapter 2). Browse production values are based on a tree density of 1000 trees/ha.

Species Guild	**Mean browse production (% of LDM (kg) ± SE)**	
	growing season	**non-growing season**
Deciduous:		
Acacia nilotica	55.36 ± 23.12	4.38 ± 1.57
Semi-deciduous:		
Spirostachys africana	409.07 ± 96.44	59.63 ± 14.47
Evergreen:		
Euclea divinorum	156.28 ± 33.76	36.74 ± 10.35
Gymnosporia senegalensis	7.34 ± 1.75	2.60 ± 0.61

Rainfall and temperature

According to Scholes (1997), the availability of water to plants, in southern African savannas, is the switch that determines the period of time for which they can grow, and nutrient availability is the rheostat regulating the rate of production when the switch is on. Growth is initiated in woody plants in response to temperature and day-length changes in the late dry season, but only if residual soil moisture is sufficient (Dekker and Smit 1996, Scholes and Walker 1993).

Little information is available on the link between total annual rainfall and differences in browse production between sites. Le Hourerou (1980) showed a positive relation between total annual rainfall and total woody plant production within arid areas in northern Africa. According to Rutherford (1984), woody production in a dystrophic, broad-leafed savanna (c 630 mm annual rainfall) was unaffected by rainfall in the current or previous year, except in drought years, and thus may be buffered by its links to soil moisture reserves. Our study confirmed Rutherford’s result in that rainfall was not found to be a factor determining browse production in any of the models produced.

According to Adcock (2001), a plant’s production rate is constrained by its N metabolism. The rate of plant N up-take is related to the soil supply its N mineralization rate. This in turn is largely controlled by water availability (Adcock 2001). Scholes and Walker (1993) showed that P mineralization is also dependent on the presence of available moisture in soils.

The distribution of rainfall throughout the year is also relevant in browse production and thus browser carrying capacity. The importance of the length of the growing season in potential browse forage supply has been emphasized by Owen-Smith (1990) as well as in our studies.

Soil/ Geology

The texture (clayey vs. sandy soils) and depth (shallow vs. deep) of the soil, together with the topography (run-off vs. run-on sites) modify the effect of rainfall on water availability and therefore, plant production (Adcock 2001).

Browse production is likely to increase with increasing soil fertility. Phosphorus is an important soil-derived mineral promoting soil fertility (Adcock 2001). The availability of P can directly influence plant growth by influencing the rate at which microbial decomposers mineralise nitrogen (Adcock 2001). Deficiencies in one or more of the other essential macro and micro elements can not only slow plant growth but also affect mineralisation in soils (Reuss and McNaughton 1987). Reuss and McNaughton (1987) found that lower microbial biomasses are found in less-fertile soils, resulting in lower rates of nutrient recycling on less-fertile soils.

Differences in browse production and nutritive value between study areas

Study area, rainfall, temperature and soil physical and chemical properties were not identified by the various CART® and MARS® models presented in this study. Despite this, differences in browse production and nutritive value among the different study areas in this study were observed and we would like to report them here in keeping with the environmental and species effects on browse production and hence browser carrying capacity.

A clear difference in the production of browse of the seven tree species (*A. nilotica, C. bispinosa, D. cinerea, E. divinorum, G. senegalensis, S. africana* and *Z. mucronata*) among three study areas (BGP, MGR and PGR), situated on a distinct moisture gradient, was detected (Table 7.2). Study areas were separated by a rainfall difference of approximately 200 mm/annum, with BGP's average annual rainfall, over the project period, being 847 mm, MGR's being 806 mm and PGR's being 648 mm. Browse production of deciduous trees on BGP was approximately 10 times that on MGR, while that of evergreen trees was up to 30 times that on

MGR (Table 7.2), with a difference in cumulative annual rainfall between the sites being only 42 mm. Both properties have similar underlying geological formations, soil types and suites of browsing herbivores. The large difference in production between the study areas, therefore, is attributed, in this study, to the presence of extinct termitaria, and the resulting enhanced soil nutrient conditions on BGP (Hughes, Granger and Hill 2003 unpublished data[1]). Hotter, drier PGR is also likely to experience enhanced evaporation rates and drainage rates (soils are more sandy than on BGP), which further account for the lower browse production rates on PGR and therefore the large difference in production between study areas. Pongola game reserve, receiving approximately 150 mm of rainfall per annum less than MGR, recorded less browse production than MGR. Interestingly the browse production of semi-deciduous trees was not greater on BGP. This may be because *S. africana,* in particular, favours water rich soils and often occurs along drainage lines and river banks (Pooley 1997), as was the case in this study. Browse production in this species is therefore enhanced by higher soil moisture content (Do et al. 2005). In conclusion, the moisture gradient, as determined by rainfall and soil texture, running north south along the northern Zululand coast of KZN, has a marked affect on browse production.

Mesophyllus trees produced twice the annual browse production on PGR than do macrophyllus trees. Pongola game reserve was the driest property in this study, receiving a mean annual rainfall of approximately 650 mm. This is an important distinction, a reduction in browse production in macrophyllus trees, as a response to a reduction in rainfall illustrates that the cost of maintaining large leaves under conditions of lower rainfall, begins to have a negative feedback effect on the tree in terms of its potential to produce new material or to grow into competitive zones the following season. The potential loss of water by transpiration in mesophyllus trees is assumed to be less than that of macrophyllus trees, allowing them to be more productive and more competitive under the same conditions.

The comparison between meso- and macrophyllus trees does not apply to a comparison of micro- and mesophyllus trees (Table 7.2). This is largely because

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of the long season of deciduousness experienced by the microphyllus species, which lowers the overall comparative annual yield of this guild. Deciduous species, also tend to invest more energy into leaf production, on old existing branches, than into shoot extension (Milton 1987).

Table 7.2: Mean annual browse production (kg/ha/annum ± SE) for deciduous, semi-deciduous and evergreen trees studied over two years for each study area (BGP – Bonamanzi Game Park, MGR Mun-Ya-Wana Private Game Reserve, PGR – Pongola Game Reserve) situated along the northern Zululand coast of KwaZulu-Natal. Browse production values are based on a tree density of 1000 trees/ha. Letters above means indicate differences between seasons for each species guild (*P*<0.05).

Species	**Year**	**Mean browse production (kg/ha/annum ± SE)**			**F-ratio**	***P*-value**
		BGP	**MGR**	**PGR**		
Deciduous:						
Acacia nilotica	1	3460 ± 2833	331 ± 104	146± 29	$F_{2,14} = 0.61$	0.52
	2	4646 ± 2755	125 ± 34	523 ± 443	$F_{2,14} = 1.34$	0.30
Dichrostachys cinerea	1		36 ± 14	0.5 ± 0.2	$F_{1,4} = 2.99$	0.16
	2		43 ± 16	7 ± 4	$F_{1,4} = 2.78$	0.17
Semi-deciduous:						
Spirostachys africana	1	4248 ± 1773	7759 ± 2795	10052 ± 7677	$F_{2,12} = 0.31$	0.74
	2	6404 ± 1833	7087 ± 4727	2147 ± 330	$F_{2,12} = 0.62$	0.55
Ziziphus mucronata	1		10675^a ± 1967	3058^b ± 1919	$F_{1,8} = 6.95$*	0.03
	2		10818 ± 6429	1897 ± 1226	$F_{1,8} = 1.22$	0.30
Evergreen:						
Carissa bispinosa	1	14295^a ± 3220	833^b ± 380	498^b ± 258	$F_{2,13} = 19.45$**	0.00
	2	14600^a ± 5579	470^b ± 295	494^b ± 280	$F_{2,13} = 7.11$*	0.01
Euclea divinorum	1	22280^a ± 7500	7335^b ± 3137	2545^b ± 1735	$F_{2,15} = 4.60$*	0.03
	2	36382^a ± 11526	3683^b ± 1449	700^b ± 321	$F_{2,15} = 8.71$*	0.00
Gymnosporia senegalensis	1	156 ± 52	220 ± 49	218 ± 118	$F_{2,13} = 0.39$	0.69
	2	344 ± 156	146 ± 83	82 ± 36	$F_{2,13} = 1.04$	0.38

Importance of the browse resource during the dry season – implications for carrying capacity

In many arid and semi-arid areas of the world, uneven rainfall distribution leads to fluctuations in the quantity and nutritive value of forage available to animals. In general, forage is plentiful during and immediately after the rainy season becoming scarce during the dry season. Mixed feeders and even some grazing herbivores switch to browse when the grazing resource is exhausted or decreases in quality in the dry season (Landman and Kerley 2001, Le Houerou

1980, Aganga et al. 2000, Bourgarel et al. 2002, Attwell and Bhika 1985, Pietersen et al. 1993, Furstenburg 2005). Trees (even those that are deciduous) have longer leaf-production cycles than the herbaceous plants. The availability of grass resources is characterised by a peak in herbaceous production in the rainy season, with high N and energy content, while in the dry season, resources gradually decrease in quantity as well as in nutritive value, and are then unable to meet the maintenance requirement of the animals (Sanon 2007). The browse resource has various forage components (green and dry leaves, flowers and fruits) and a longer period of availability. Hence they constitute an essential resource for large herbivores during the long dry season and drought years. In wildlife systems, browse species constitute an effective insurance against seasonal feed shortage in the dry season, supplementing the quantity and nutritive value of grass (Sanon 2007). Trees and shrubs are perennials allowing the provision of permanent forage compared to some herbaceous species, which decrease rapidly in quantity and nutritive value after the rains. Through their deep root system, trees are able to penetrate further into the soil and therefore continue to grow under dry conditions and/or keep green leaves.

Comparisons of browse production as a percentage of browse biomass for each study area gives an idea of the relative production rates of the different tree guilds in relation to environmental differences (Table 7.3). Browse production is higher for all species (except *S. africana* during the wet season) in both wet and dry seasons on BGP. Production continues during the dry season, if only to a limited extent - even on PGR, the driest study area. In fact dry season browse production of *S. africana* and *E. divinorum* remain is comparable to the wet season production of the other study tree species. It is the carryover of wet season production into the dry season, and the continued slower dry season production that forms this important dry season forage resource for large herbivores. This resource is an essential buffer or bridge resource for browser carrying capacity.

Table 7.3: Mean wet and dry season browse production browse production (kg/ha/quarter ± SE) as a percentage of browse biomass (LDM (kg)) for each species guild in each study area (determined using the non-linear regression equations developed in Chapter 2). Browse production values are based on a tree density of 1000 trees/ha.

Species Guild	**Season**	**Mean browse production (% of LDM (kg) ± SE)**		
		BGP	**MGR**	**PGR**
Deciduous:				
A. nilotica	wet	93.18 ± 41.00	10.12 ± 3.02	6.29 ± 4.26
	dry	6.17 ± 2.85	2.61 ± 0.64	1.33 ± 0.83
Semi-deciduous:				
S. africana	wet	362.16 ± 113.48	526.29 ± 134.81	343.31 ± 252.97
	dry	72.78 ± 29.00	72.00 ± 32.42	52.15 ± 18.83
Evergreen:				
E. divinorum	wet	206.11 ± 39.39	75.57 ± 22.64	22.20 ± 9.44
	dry	34.51 ± 12.91	21.27 ± 7.19	23.51 ± 11.03
G. senegalensis	wet	10.02 ± 3.08	6.86 ± 3.058	4.67 ± 2.17
	dry	1.56 ± 0.46	4.75 ± 1.48	1.57 ± 0.55

Daily CP requirements for maintenance for an adult impala (45 kg) were met by all species over all three study sites and all seven seasons. Daily CP requirements for growth and lactation, however, were only ever met by deciduous and semi-deciduous species.

Main conclusions

Browse biomass

- Canopy volume proved to be a useful measure of tree biomass, provided foliage densities are estimated accurately.
- The proposed non-linear regression models for estimating the available leaf mass for browsers are useful in their management and the monitoring of their effect on the available leaf material over a period.

Browse production

- Available canopy volume, height to the lowest leaves of the canopy, tree species and season were the most significant determinants of browse production

- Browse production for the different study tree species was markedly different resulting in the need to group species into phenological guilds: evergreen, semi-deciduous and deciduous.
- Evergreen trees (with the exception of *G. senegalensis*) consistently maintained greater browse production than deciduous trees, across both study years and all seven sampling seasons.
- The effect of quarterly defoliation on browse production was greater during the growing season, than in any other season, and had a lasting effect over the rest of the year.
- Evergreen, deciduous and semi-deciduous trees consistently produced greater amounts of browse up the canopy, with the 2.5–5 m feeding level recording the greatest browse production and the 0-0.5 m feeding level the least.
- Browse production during the growing season essentially determines the amount of browse available to mammalian herbivores in the year ahead, as well as the tree's ability to respond to the defoliation (or any other stress for that matter) of the previous season. Comparing the browse production figures during the growing season of consecutive years would supply land managers with valuable insight into whether the browse component of the system is under stress, is maintaining, or perhaps is encroaching.
- The length of the growing season has a marked effect on the production potential of savanna tree species. In determining the browsing capacity of an area, the length of the growing season will have a profound effect on the capacity of the area to sustain more browsers.

Browse nutritive value

- A consistent difference was established between the browse nutritive value of evergreen species and deciduous species (of varying shades), where deciduous species showed the greatest nutrient concentrations and lowest concentrations of fibre.
- The influence of study area on browse nutritive value and hence browser selection, could not be established. The ADF concentrations of all tree

guilds (deciduous, semi-deciduous and evergreen), however, were greater on BGP, the wettest study area. Crude protein concentrations, by contrast were greatest for all tree guilds, on PGR – the driest study area.

- Browse nutritive value was greatest during the wet season, when growth and photosynthesis are at their greatest. Indeed, ADF levels were lower while CP concentrations were greater during the wet seasons. Furthermore, ADF concentrations were greater and CP concentrations were less during the first, and drier, year of sampling.

Browse production models

- The most significant predictors of the production of browse in deciduous, semi-deciduous and evergreen trees were measurable plant dimensions, namely: available canopy volume, tree height, stem diameter, height to the lowest leaves of the canopy and foliage density.
- Tree growth (and therefore tree size and shape), although related to the life form history and genetics of each species, is also largely determined by a number of environmental factors (discussed above). The use of tree physical dimensions to determine browse production (and browser carrying capacity) therefore encompasses the prevailing environmental effects indirectly.

Research Gaps highlighted and possible areas of future research

- Determining whether further stratification (including browse feeding levels in browse production models, differentiating between shoot types – i.e. leader, vs 2^o, 3^o etc.) will reduce the extreme variability associated with browse production measures.
- How do leaf litter and seed pods/fruit fit into browse carrying capacity? If consumed by browsers, litter yield would skew the carrying capacity equation in favour of deciduous over evergreen trees.
- Is soil water moisture more strongly related to browse production compared to mean monthly rainfall? This relation is predicted to be strongest at the start of the growing season prior to rainfall.

- Competition effects (specifically shading effects, although there are numerous others) on tree size, canopy volume and foliage density and resultantly on browse production.
- Browsing effects on production, specifically the difference in wet/dry season browsing on production.
- Related to browsing effects on production is the influence of secondary defences on browse production. Does the presence of secondary metabolites in the leaves of browsed trees reduce or enhance browse production?

Main recommendations for carrying capacity determination

On the assumption that browse production equates to utilisable browse biomass, our study has provided managers with 3 general species guild models (Chapter 6) to determine browse production at the beginning of the growing season. Relating the determined browse production figures for the tree species assemblages on a property in question to the daily required forage intake of a specific browsing herbivore/s (Pietersen et al. 1993) will yield an estimate of the number of animals that may be supported by the browse resource for the year ahead. Repeating these measurements annually, provides a useful monitoring tool of vegetation health. Furthermore the use of the ACVol calculation method outlined in Chapters 2 and 3, allows for the determination of ACVol sizes specific to the browsing heights of different browsing herbivores, allowing for the more accurate prediction of utilisable browse production for different browsing herbivores.

Final comments

This study explored the key factors affecting browse production, biomass and nutritive value and in turn, used these factors to develop models to assess and monitor these parameters across seasons and properties. The identification of the key factors affecting aspects of browse quantity and nutritive value and the resultant models developed have improved our understanding of browse dynamics in southern African savannas and have provided a more ecologically sound platform for the determination of browser carrying capacities.

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