

The dependence of herbivory on growth rate in natural plant communities

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Summary

1. The hypothesis that herbivory pressure (defined as the per cent of the photosynthetic tissue biomass and production consumed daily by herbivores) increases with increasing plant growth rate was tested. The basis for the test was a compilation of 56 published reports on biomass, production and herbivory, from a wide range of aquatic and terrestrial plant communities.
2. Herbivory was independent of ecosystem primary production and the fraction of plant production and biomass daily consumed by herbivores increased as the 0.6 and 1.6 power of plant turnover rate, respectively.
3. These results suggest that the tendency of fast-growing plants to support lower biomass of photosynthetic tissues than slow-growing ones can be accounted for by the tendency of herbivore control of plant biomass and production to increase with increasing plant growth rate.
4. It is concluded that herbivory should be most important as a control mechanism for fast-growing plant communities, whereas it represents but a modest percentage of losses of photosynthetic tissues of slow-growing plants.

Key-words: Plant–animal interactions, plant defences, plant production

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Introduction

Plant production can be consumed as live material by herbivores or as dead material by decomposers (i.e. bacteria, fungi and associated animals). A fundamental difference between these two paths is that detritivores can only influence plant production indirectly through their effect on nutrient cycling, for they act upon dead plant material, whereas herbivores may exert a direct controlling effect, whether positive (Porter 1976; McDonald 1985; Carpenter 1986) or negative (Lein 1980; Edwards 1985; Feminella & Resh 1989). The extent of herbivore control of plant production, also referred to as top-down control of primary production, should depend, therefore, on the fraction of the plant production removed by herbivores. Hence, this role has been best demonstrated for communities heavily consumed by herbivores, such as some African grasslands (McNaughton 1984; McNaughton & Georgiadis 1986; Maschinski & Whitham 1989) and phytoplankton communities (Lampert *et al.* 1986; Frost 1991).

Comparative analyses of the extent of herbivory in different ecosystems have demonstrated a linear relationship between ecosystem primary production and herbivory rate, both in terrestrial (McNaughton *et al.* 1989) and aquatic (Cyr & Pace 1993) ecosystems.

These analyses indicate that the proportion of plant production removed by herbivores does not vary in any consistent way with ecosystem production (Cyr & Pace 1993). Indeed, the fraction of ecosystem production consumed by herbivores varies as much as 1000-fold for ecosystems with similar primary productions (e.g. McNaughton *et al.* 1989; Cyr & Pace 1993), although there is a tendency for a greater fraction of primary production to be transferred to herbivores in aquatic than in terrestrial ecosystems (Petrušewicz & Grodzinski 1975; Cyr & Pace 1993). Hence there are, at present, no patterns accounting for the large differences in the fraction of production consumed by herbivores in different ecosystems. This information would, however, be instrumental in identifying those communities or ecosystems where top-down control of ecosystem production dominates over bottom-up regulation (i.e. resource control).

Independent research, both in aquatic (Riemann *et al.* 1990) and terrestrial (Mooney & Gulmon 1982; McNaughton, Ruess & Seagle 1988; Landsberg & Ohmart 1989; Jing & Coley 1990) ecosystems, has provided evidence that fast-growing plants are subject to intense herbivory pressure but that herbivores consume a small fraction of the production of slow-growing plants (Bray 1964; Petrušewicz & Grodzinski

1975). This tendency has been also postulated for terrestrial plant species (Coley, Bryant & Chapin 1985; Bryant *et al.* 1989), on the grounds that fast-growing plants should be more palatable to herbivores than slow-growing plants. This contention is based on observations that fast-growing plants tend to have high nutrient contents and low levels of defence chemicals (Klopatek & Stearns 1978; Mattson 1980) compared to the poor nutritional quality and high levels of defence chemicals often encountered in slow-growing plants (Landsberg & Ohmart 1989). There are, however, exceptions to this pattern, as some fast-growing plants may produce defence chemicals as a result of coevolution with herbivores (Edwards 1989). The hypothesis that the extent of herbivory among different ecosystems increases as the growth rate of the dominant primary producers increases, would, if confirmed, provide a basis to predict which communities are more likely to be subject to top-down control of their primary production,

thereby improving our understanding of plant-herbivore interactions.

Here, we examine the hypothesized relationship between herbivory pressure and plant growth rate, based on published data. We first confirm previous findings (McNaughton *et al.* 1989; Cyr & Pace 1993) that the proportion of the production removed by herbivores does not vary in any consistent way with ecosystem production. We then show the strong positive relationship between plant growth rate and the fraction of their biomass and production removed by herbivores.

Materials and methods

We searched the literature for data on herbivory rates across communities spanning the broadest possible range in growth rate of the dominant primary producers (Table 1). Unfortunately, reports of growth rate and herbivory of below-ground (roots and rhizomes)

Table 1. Plant communities and dominant species, in the data set on grazing rates, biomass and production compiled

System	Plant community and species	Location	Reference
Marine	Phytoplankton		
	Mixed community	Central Pacific Gyre	Welschmeyer & Lorenzen (1985)
	Mixed community	Washington (USA)	Welschmeyer & Lorenzen (1985)
	Mixed community	Alaska (USA)	Lawes <i>et al.</i> (1988)
	Macroalgae		
	<i>Cystoseira barbata</i>	Black Sea	Khailov & Burlakova (1969)
	<i>Dilophus fasciola</i>	Black Sea	Khailov & Burlakova (1969)
	<i>Cladostephus verticillatus</i>	Black Sea	Khailov & Burlakova (1969)
	<i>Polysiphonia subulifera</i>	Black Sea	Khailov & Burlakova (1969)
	<i>Callithamnion corymbosum</i>	Black Sea	Khailov & Burlakova (1969)
	<i>Ceramium rubrum</i>	Black Sea	Khailov & Burlakova (1969)
	<i>Ceramium diaphanum</i>	Black Sea	Khailov & Burlakova (1969)
	<i>Laurencia obtusa</i>	Black Sea	Khailov & Burlakova (1969)
	<i>Cladophora</i> sp.	Black Sea	Khailov & Burlakova (1969)
	<i>Enteromorpha</i> sp.	Black Sea	Khailov & Burlakova (1969)
	Seagrasses		
	<i>Thalassia testudinum</i>	Caribbean Sea	Gallegos <i>et al.</i> unpublished results
	<i>Zostera noltii</i>	Dutch Wadden Sea	Jacobs <i>et al.</i> (1981)
	<i>Zostera marina</i>	the Netherlands	Nienhuis & Groenendijk (1986)
	Freshwater	Phytoplankton	
Mixed community		Norway	Hessen, Andersen & Lyche (1990)
Mixed community		Norway	Vadstein <i>et al.</i> (1989)
Mixed community		Germany	Lampert <i>et al.</i> (1986)
Mixed community		Denmark	Christoffersen <i>et al.</i> (1990)
Mixed community		Germany	Platzek (1991)
Bentic diatoms			
<i>Gleotridia</i> sp. and <i>Mogeotia</i> sp.		Canada	Cattaneo (1983)
<i>Synedra</i> sp. and <i>Cymbella</i> sp.		Michigan (USA)	Hunter (1980)
Submerged macrophytes			
<i>Potamogeton pectinatus</i>	the Netherlands	Van Wick (1988)	
Marsh	Emergent plants		
	<i>Nuphar luteum</i>	Georgia (USA)	Wallace & O'Hop (1985)
	<i>Juncus roemerianus</i>	Georgia (USA)	Parsons & de la Cruz (1980)
	<i>Spartina alterniflora</i>	Georgia (USA)	Smalley (1960)
	<i>Spartina alterniflora</i>	Maryland (USA)	Cahoon & Stevenson (1986)
	<i>Hibiscus moscheutos</i>	Maryland (USA)	Cahoon & Stevenson (1986)

Table 1. (Continued)

System	Plant community and species	Location	Reference
Terrestrial	Grasslands		
	<i>Artemisia tridentata</i> community	Eastern Idaho (USA)	Pearson (1965)
	Shortgrass prairie	Colorado Desert (USA)	Scott, French & Leetham (1979)
	Mixed prairie	South Dakota (USA)	Scott <i>et al.</i> (1979)
	Tallgrass prairie	North-east Oklahoma (USA)	Scott <i>et al.</i> (1979)
	Desert grassland	New Mexico (USA)	Scott <i>et al.</i> (1979)
	<i>Themeda triandra</i> community	Tanzania	Sinclair (1975)
	<i>Digitaria macroblephora</i> community	Tanzania	Sinclair (1975)
	<i>Erodium cicutarium</i>	California (USA)	Soholt (1973)
	<i>Festuca arundinacea</i> and <i>Andropogon virginicus</i>	Tennessee (USA)	Van Hook (1971)
	<i>Themeda triandra</i> community	Kenya	Cox & Whaitaka (1989)
	<i>Bothriocloa insculpta</i> community	Kenya	Cox & Whaitaka (1989)
	<i>Sericea lespedeza</i>	South Carolina (USA)	Menhinick (1967)
	<i>Puccinellia phryganodes</i>	Canada	Cargill & Jefferies (1984)
	<i>Carex subspatheacea</i>	Canada	Cargill & Jefferies (1984)
	Shrubs		
	<i>Larrea tridentata</i>	Arizona (USA)	Chew & Chew (1970)
	Taiga forest shrub community	Alaska (USA)	Grodzinski (1971)
	Trees		
	<i>Acacia</i> spp. and <i>Commiphora</i> spp.	Tanzania	Sinclair (1975)
	<i>Kandelia candel</i>	Hong Kong	Lee (1991)
	<i>Betula pubescens</i> spp. <i>tortuosa</i>	Norway	Wielgolaski (1975)
	<i>Eucalyptus delegatensis</i>	Australia	Ohmart, Stewart & Thomas (1983)
	<i>Eucalyptus dives</i>	Australia	Ohmart <i>et al.</i> (1983)
	<i>Eucalyptus pauciflora</i>	Australia	Ohmart <i>et al.</i> (1983)
	<i>Pseudotsuga castanopsis</i> community	Oregon (USA)	Grier & Logan (1977)
	<i>Pseudotsuga castanopsis</i> community	Oregon (USA)	Grier & Logan (1977)
	<i>Pseudotsuga-Rhododendron-Gaultheria</i>	Oregon (USA)	Grier & Logan (1977)
	<i>Pseudotsuga-Rhododendron-Berberis</i>	Oregon (USA)	Grier & Logan (1977)
<i>Pseudotsuga-Acer-Polystichum</i>	Oregon (USA)	Grier & Logan (1977)	
Mixed community	New Hampshire (USA)	Gosz <i>et al.</i> (1978)	

and woody parts (branches and trunks) were few. Hence, we restricted our analysis to the biomass, production and herbivory of green plant material, and excluded roots, rhizomes, branches and trunks, which are generally subject to lower herbivory pressure than green parts (Gosz *et al.* 1978; DeAngelis, Gardner & Shugart 1981). Hence, the terms biomass and production refer to green parts alone hereafter. We represented relative plant growth rate as the turnover rate (p/B , i.e. production per unit of green plant biomass per day, units day^{-1}), which is the descriptor of plant growth rate most often reported in the literature. We described herbivory pressure on the plants as both the fraction of the green plant biomass and production removed daily by herbivores. This study was limited to natural communities, thereby avoiding experimental manipulations and herbivory by livestock. Herbivory rates on or by individual species were accepted only when these species dominated community biomass and production, or herbivory rates, respectively. Biomass values were converted, when given in different units, to $\text{g dry weight m}^{-2}$ and production values to $\text{g dry weight m}^{-2} \text{day}^{-1}$.

The relationships between variables were tested using least squares regression analyses on log-transformed variables. Logarithmic transformation was

necessary, as in similar studies (McNaughton *et al.* 1989; Cyr & Pace 1993), to comply with the assumptions of the analysis. The relationships between ratios involving a common variable in the independent and dependent ratios were tested for spurious results (i.e. relationships solely derived from the presence of a common variable in both ratios: Chayes 1971; Atchley & Anderson 1978; Kenney 1982) using a randomization test (Pendleton, Newman & Marshall 1983).

Results and discussion

The data set comprised 56 reports of plant production and herbivory pressure on a broad range of marine (phytoplankton, macroalgae and seagrasses), marsh, freshwater (phytoplankton, periphyton, submerged macrophytes) and terrestrial (grasses, shrubs and trees) plant communities (Table 1). These communities ranged widely in biomass and production (about six and four orders of magnitude, respectively). Biomass of photosynthetic tissues increased from planktonic communities to forests (Fig. 1), unlike production, as leaf production in some forests was similar to the production of some phytoplankton communities (Fig. 1). Thus, production (p) was not lin-

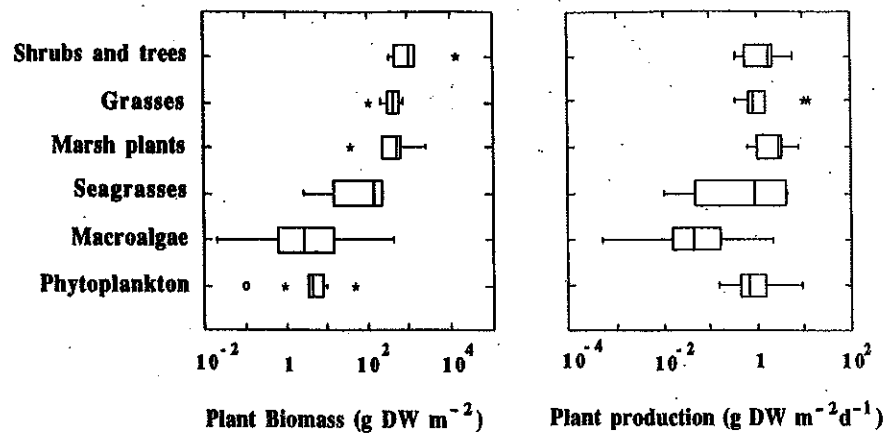


Fig. 1. Box plots comparing the distribution of biomass and production for the different plant types in the data set. Boxes encompass 25% and 75% quartiles, and the central line represents the median, and bars encompass 95% of the values. Asterisks and open circles indicate observations outside the 95% limits.

early scaled to plant biomass (B), as indicated by the regression equation:

$$\log p \text{ (g dry wt m}^{-2} \text{ day}^{-1}) = -1.17 + 0.50 (\pm 0.06) \log B \text{ (g dry wt m}^{-2})$$

$$(r^2 = 0.57, n = 56, F = 72.9, P < 0.0001)$$

This equation indicated that production increases more slowly than plant biomass among different plant communities (Student's t -test; H_0 , slope=1, $P < 0.001$). Analyses of covariance revealed that most of the variance in plant production in the data set was attributable to differences in plant biomass ($F = 101$, $P < 0.0001$), compared to smaller, albeit significant ($F = 14.8$, $P < 0.001$), differences among communities. The relationship obtained indicated that plant growth rate (as turnover rate) decreases with increasing plant biomass ($r = -0.75$; Fig. 2). Hence, community primary production per unit area is a poor descriptor of the growth rate of the component plants, as high primary production may be achieved by dense communities of slow-growing plants (e.g. forests) or by fast-growing sparse plant communities (e.g. phytoplankton; Fig. 1).

Herbivory rates varied substantially, from about 10⁻⁵% to >50% of the photosynthetic biomass removed daily, across the plant communities in the data set (Fig. 3) and differed significantly across the communities examined (ANOVA, $F = 39.7$, $P < 0.0001$). Herbivory rates were greatest in some phytoplankton communities, where all the production was removed by herbivores and smallest in some forests where herbivores removed less than 1% of production (Fig. 3). These differences were not explained by differences in ecosystem primary production, as the fraction of the production consumed by herbivores ranged widely (from <1% to 100%) for communities with similar primary production (Fig. 4). That the fraction of the primary production consumed by herbivores is weakly related to ecosystem primary production ($r = -0.29$, $P = 0.03$; Fig. 4) is in accord with previous findings

(McNaughton *et al.* 1989; Cyr & Pace 1993). This indicates that ecosystem primary production is also a poor indicator of the importance of herbivore control on photosynthetic plant biomass and production.

The difference in the proportion of primary production consumed by herbivores among different plant communities was associated to a tendency for herbivory pressure to increase with increasing plant growth rate (Fig. 5). Regression analysis indicated that the proportion of the production consumed by herbivores tended to increase as the 1/2 power of plant turnover rate (Fig. 5), as described by the regression equation:

$$\log \% \text{ production consumed by herbivores} = 2.27 + 0.59 (\pm 0.086) \log p/B \text{ (day}^{-1})$$

$$(r^2 = 0.46, n = 56, F = 47.0, P < 0.0001)$$

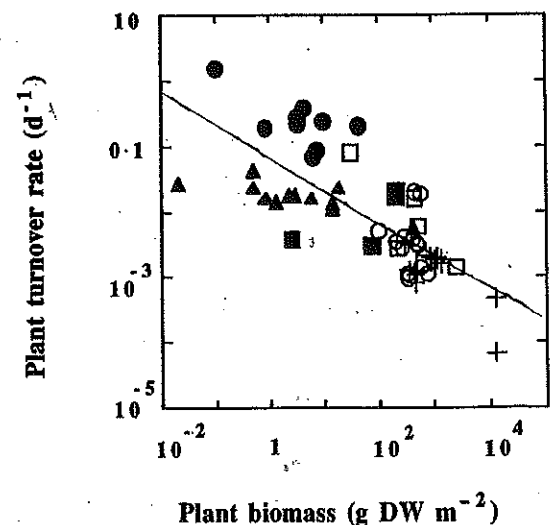


Fig. 2. The relationship between plant turnover rate and plant biomass. Symbols represent phytoplankton (●), macroalgae (▲), seagrasses (■), marsh and freshwater plants (□), grasses (○), and shrubs and trees (+), and the solid line represents the fitted regression equation.

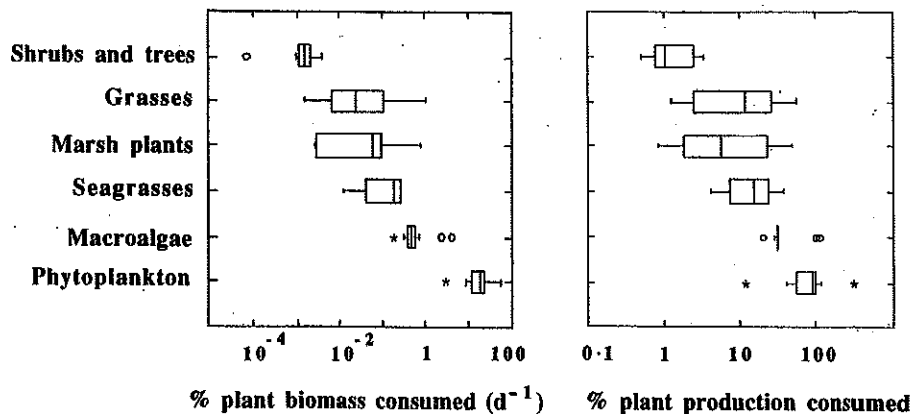


Fig. 3. Box plots comparing the distribution of the proportion of the biomass and production consumed by herbivores per unit time for the different plant types in the data set. Boxes encompass 25% and 75% quartiles, the central line represents the median and bars encompass 95% of the values. Asterisks and open circles indicate observations outside the 95% limits.

The slope of the observed relationship differed significantly (Student's *t*-test, $P < 0.0001$) from that expected if it was a spurious result of using plant production in the denominator and numerator of the dependent and independent variables, respectively (-0.36 ± 0.01 , randomization test). This relationship indicates that herbivores consume most, or all, of the production of plant communities doubling their biomass faster than once a week, whereas this is $< 1\%$ of the production of plant communities with turnover times of 1 year and longer (Fig. 5). Fast-growing plant communities support, therefore, a disproportionately larger herbivory pressure than slow-growing ones, implying that herbivores should exert a stronger control on the biomass of fast-growing, compared to slow-growing, plant communities. This was also indicated by the tendency of the proportion of the biomass consumed by herbivores per unit time to increase as the $3/2$ power of plant turnover rate (Fig. 5), as described by the regression equation:

$$\log \% \text{ plant biomass consumed by herbivores day}^{-1} \\ = 2.35 + 1.61 (\pm 0.09) \log p/B (\text{day}^{-1})$$

$$(r^2 = 0.83, n = 56, F = 270, P < 0.0001)$$

Hence, herbivores remove a disproportionate fraction of the biomass of fast-growing plant community per unit time than that they remove from slow-growing communities. The slope obtained also differs significantly (Student's *t*-test, $P < 0.0001$) from that expected (0.93 ± 0.007 , randomization test) if the relationship were spurious, derived from the use of plant biomass to calculate both the proportional biomass consumed by herbivores and plant turnover. A minor (9%) fraction of the differences in herbivory rate among different communities persisted after accounting for differences in their growth rate (ANOVA, $F = 6.9$, $P < 0.01$). Thus, our results support the hypothesis that fast-growing communities support greater herbivore pressure than slow-growing communities, but indicate that other factors, accounting

for the variance unexplained by differences in growth rate, must also influence this relationship.

Our results suggest that the greater biomass often accumulated by slow-growing communities (Fig. 2) should be, at least in part, a consequence of the smaller herbivory pressure they experience. Partial correlation analysis showed this to be the case, as the strong, negative relationship between plant turnover and biomass ($r = -0.75$) was considerably reduced ($r = -0.30$), albeit still significantly ($P < 0.05$), when accounting for differences in herbivory pressure. Hence the tendency for plant biomass to decrease with increasing turnover cannot be explained by differential herbivory alone and indicates the importance of other factors such as the growth form or allocation strategies of the plants.

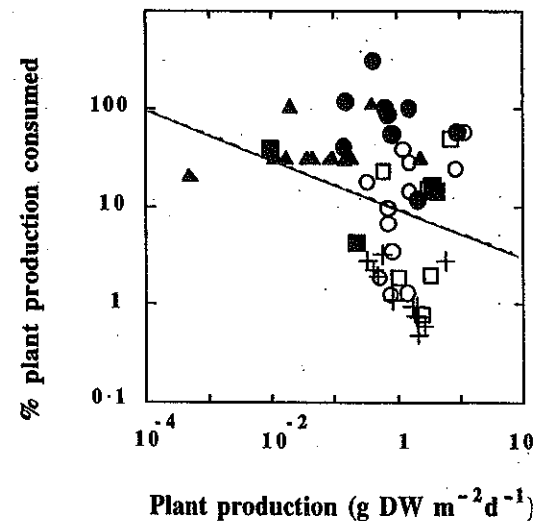


Fig. 4. The relationship between the per cent production consumed by herbivores and primary production. Symbols represent phytoplankton (●), macroalgae (▲), seagrasses (■), marsh and freshwater plants (□), grasses (○), and shrub and trees (+), and the solid line represents the fitted regression equation.

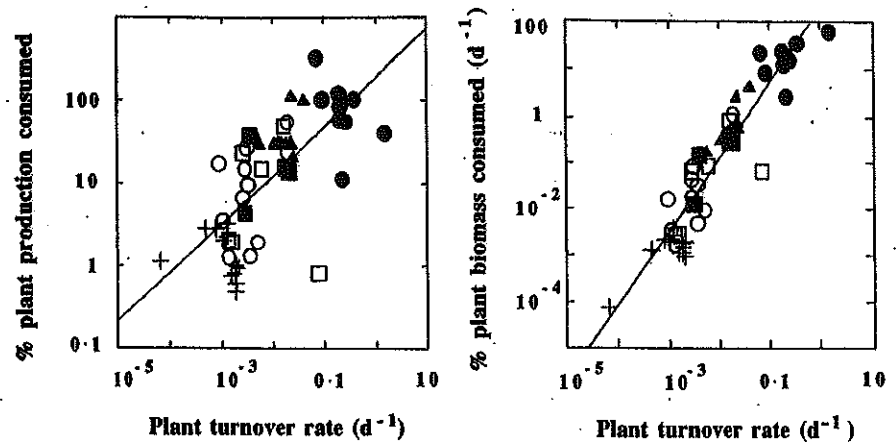


Fig. 5. The relationship between the per cent production and biomass consumed daily by herbivores and plant turnover rate. Symbols represent phytoplankton (●), macroalgae (▲), seagrasses (■), marsh and freshwater plants (□), grasses (○), and shrubs and trees (+), and the solid line represents the fitted regression equations.

The results obtained confirm the hypothesized increase in herbivory pressure with increasing plant growth rate. That the fraction of the biomass or production removed by herbivores is independent of community primary production is a consequence of the fact that primary production is independent of plant growth rate. These results stress the importance of plant growth rates in accounting for differences in herbivory pressure among ecosystems. Herbivores should exert a stronger control on the biomass and production of fast-growing plant communities, probably because the high-nutrient, protein and nucleic acid levels needed to support fast plant growth, which render fast-growing plants attractive food items to herbivores (Coley 1980; Sheldon 1987). In contrast, herbivores consume a moderate fraction of the production and biomass of green tissues of slow-growing plants, consistent with the tendency for these plants to have low-nutrient content and carbon compounds relatively unpalatable to herbivores (Mattson 1980; Coley *et al.* 1985; Landsberg & Ohmart 1989). Hence, most of the production of slow-growing communities should enter the detrital food chain, suggesting that their biomass and production should be primarily regulated by resource availability and its recycling by decomposers.

These generalities, while useful in accounting for broad-scale patterns in herbivory pressure among different communities, have remarkable exceptions: for example, the great herbivory pressure exerted on trees during insect outbreaks (Gosz *et al.* 1978; Schowalter, Hargrove & Crossley 1986; Potter & Redmond 1989), the ability of sea-urchins to eliminate kelp communities during population blooms (Ogden 1976; Kirkman & Young 1981), the very high herbivory pressure (>90%) large herbivores may be able to exert on African grasslands (McNaughton 1985) and the low herbivory rates observed for some fast-growing

phytoplankton and macroalgae containing toxic substances (e.g. Paerl 1988).

In summary, our results support the hypothesis that herbivory pressure increases with increasing plant growth rate. Thus, while ecosystems with high primary production should be able to support high herbivore production (Coe, Cumming & Phillipson 1976; McNaughton *et al.* 1989; Cyr & Page 1993), herbivores tend to exert a greater pressure on the biomass and production of fast-growing, compared to slow-growing communities.

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