Estimating patterns of leaf herbivory along an altitudinal transect in NE Queensland rainforests: might global warming increase leaf herbivory in tropical rainforests?

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Abstract. Climate change has been taking place at unprecedented rates over the past decades. These fast alterations caused by human activities are leading to a global warming of the planet. Warmer temperatures are going to have important effects on vegetation and especially on tropical forests. Insects as well will be affected by climate change. This study tested the hypothesis that higher temperatures lead to a higher insect pressure on vegetation. Visual estimations of leaf damage were recorded and used to assess the extent of herbivory in nine 0.1ha plots along an altitudinal gradient, and therefore a temperature gradient. These estimations were made at both a community level and a species level, on 2 target species. Leaf toughness tests were performed on samples from the target species from each plot. Results showed a strong evidence of increasing insect damage along increasing temperature, with no significant effect from the leaf toughness.

Keywords: *Australia, climate change, herbivory, plant-animal interaction, tropical rain forest.*

Resum. El canvi climàtic està tenint lloc des de fa dècades a un ritme sense precedents. Aquestes ràpides alteracions causades per l'activitat humana comporten a un escalfament global del planeta. Temperatures més altes tindran efectes importants sobre la vegetació i en especial sobre els boscos tropicals. Els insectes també es veuran afectats pel canvi climàtic. Aquest estudi ha testat la hipòtesi que temperatures més altes comporten una major pressió dels insectes sobre la vegetació. Es van anotar i fer servir estimacions visuals del dany a les fulles en nou parcel·les de 0.1ha en un gradient altitudinal, i per tant, en un gradient de temperatura. Aquestes estimacions varen ser fetes tant a nivell de comunitat com a nivell d'espècies, a dues espècies objectiu. Es van fer proves de duresa foliar en mostres de les espècies objectiu de cada parcel·la. Els resultats mostren una forta evidència d'augment del dany per part dels insectes al mesura que augmenta la temperatura, amb cap afecte significatiu de la duresa foliar.

Paraules clau: *Austràlia, canvi climàtic, herbivoria, interacció planta-animal, boscos tropicals.*

Resumen. El cambio climático está teniendo lugar des de hace décadas a un ritmo sin precedentes. Estas rápidas alteraciones causadas por la actividad humana conllevan a un calentamiento global del planeta. Temperaturas más altas tendrán efectos importantes sobre la vegetación, y en especial, sobre los bosques tropicales. Los insectos también se verán afectados por el cambio climático. Este estudio ha testado la hipótesis que temperaturas más altas conllevan una mayor presión de los insectos sobre la vegetación. Se anotaron estimaciones visuales del daño en las hojas en nueve parcelas de 0.1ha en un gradiente altitudinal y por lo tanto, de temperatura. Estas estimaciones fueron hechas tanto a nivel de comunidad como a nivel de especies, con dos especies objetivo. Se hicieron pruebas de dureza foliar en muestras de las especies objetivo de cada parcela. Los resultados muestran una fuerte evidencia de aumento del daño por parte de los insectos a medida que aumenta la temperatura, sin ningún efecto significativo de la dureza foliar.

Palabras clave: *Australia, cambio climático, herbivoría, interacción planta-animal, bosques tropicales.*

Introduction

Climate change is a fact that cannot be negated at this point. It is happening and it can have devastating effects. Human activities are driving a global warming process that might raise the temperature of the Earth up to 6ºC in 2070 (IPCC, 2008).

This global warming episode can be especially important for terrestrial vegetation. Species adapted to one particular area would have to move to other areas (usually upland areas) looking for cooler temperatures. Concentrations of carbon dioxide would also increase in the predicted scenarios, and this would also lead to plant changes: Increased CO2 concentrations may result in growth performance and secondary changes in plant phenology due to changes in carbon assimilation (Puhe, 2001). Rainfall patterns might be altered affecting tropical areas through long periods of drought (Mahli and Wright, 2004)

The effect of climate on vegetation is not unidirectional, as vegetation can also influence climate (Raunkiaer, 1934; Holdridge, 1947; in Grime, 1997). Land carbon cycles are the most important contributors to the uncertainty about CO_2 emissions in the 21st century after the anthropogenic sources (Meir et al., 2006). Loss of forest masses would mean losing the sink for 45% of the terrestrial carbon in the Earth (Bonan, 2008). Forest loss due to climate change would have several effects on climate at the regional scale (and in a global scale if the forest loss is massive) such as an increasing surface reflectance (almost offsetting cloud effect) (Bala et al, 2007 in Mahli et al. 2007), less water re-circulation (roots absorbing water from the soil and being returned to the atmosphere), and changes in surface roughness (Mahli et al., 2007). It is known that the evaporative surfaces provided by vegetation are driving forces of the atmospheric humidity and rainfall patterns (Grime, 1997).

In the case of tropical forests, climate change would be especially fatal: although tropical forest areas only cover approximately 6-7% of the total earth's surface (Stork, N. E et al., 2008) they sequester about 40% of the carbon dioxide that is not taken by the oceans (Raven, P. H., 2008). The Wet Tropics of Queensland are one of the most ancient rainforest areas in the Earth. It contains more than 3,000 species in 210 families, with more than 50 endemic species to the area. This uniqueness makes it especially sensitive to the expected climate changes during the next 20 or 30 years. It is believed that a raise in 1ºC may reduce the rainforest area by 50% (Climate change impacts on biodiversity in Australia: outcomes of a workshop, 2002). In the Wet Tropics bioregion, the expected climate change scenarios may lead to a significantly decrease of the upland rainforest (Hilbert et al., 2001).

All the predicted climate change effects will also influence the plant-animal interaction. In particular, insect herbivory will be undoubtedly affected by the climate change. Insect herbivory is a basic part of all the nutrient cycles, webs and diversity that are a part of the rainforest operation. In this study, we will focus on the effects of temperature on the insect-plant interaction.

Many studies show that insect herbivory is much more important in tropical forests than in temperate ones for broad-leaved forests (Coley and Barone, 1996; Coley and Aide, 1991; Coley and Kursar, 1996). Generally, tropical forests species have greater resistance than do temperate species, though herbivory rates remain high. That leads us to the conclusion that herbivory pressure is higher in tropical forests than in temperate ones. Therefore, this fact may give us explanation for other similar dynamics occurring in the forest, such as tree mortality, which is higher at warmer temperatures (Hilbert et al. 2009). It is known that secondary chemicals are more important for plant defence against insect herbivores than their physical defences (Hartley, 2007). Therefore we would expect damage rates not to be correlated with leaf toughness.

Many studies have related herbivory along latitudinal gradients (Andrew N. R., et al., 2005; Coley et al., 1996, Hallam A. et al., 2006), but few have investigated the relationship with an altitudinal gradient (e.g.: Scheidel et al., 2003). Temperature is the most important abiotic factor affecting herbivory and therefore changes in altitude or longitude might affect seriously the herbivory intensity and thus, the forest dynamics.

This study tested the hypothesis that **the intensity of insect herbivory is positively correlated with decreasing altitude.** We expect the herbivory rates to increase with decreasing altitude, due to higher temperatures at lower stages. It is known that high temperature leads to higher diversity of insect herbivores and higher intensity of these at fixed latitude –higher metabolic rates, several life cycles in season- (Bale, J. S., et al., 2002). This is supported by other studies which have investigated herbivory rates along a latitudinal gradient, and therefore temperature gradients increasing towards the equator (e.g. Andrew N. R., et al., 2005; Coley et al., 1996).

Materials and methods

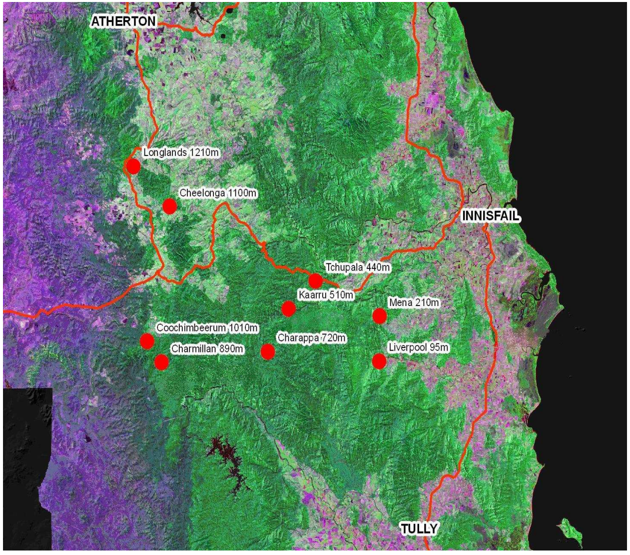
Study sites

We studied the herbivory patterns in 9 of the 12 climate-change monitoring plots that the CSIRO – Tropical Forest Research Centre (TFRC) has established in the Wet Tropics area. They are set in an altitudinal gradient from 25m to 1210m ASL, with approximately 100m of elevation between each plot. The plots are 50x20m, so each plot has a surface of 0.1ha. Within every plot, all trees of 10cm (dbh) or more were tagged and are permanently marked and all the vascular plants present have been recorded. These plots are used for forest monitoring, weed, disease and mosquito studies. Map 1 shows the Wet Tropics Area in NE Queensland, and Map 2 shows the location of the 9 monitoring plots. In Table 1 there are the most relevant characteristics of the studied sites. 3 of the 12 climate change plots were not sampled due to absence of the study species or the high disturbance caused by cyclone Larry in 2006.

Table 1: Location, altitude, basal area and number of trees of the 9 monitoring plots.

Plot name	Latitude (GDA)	Longitude (GDA)	Altitude (m)	Basal Area	Number of Trees
Liverpool	-17.71	145.86	95	35.71	91
Mena	-17.65	145.86	210	39.01	75
Tchupala	-17.60	145.76	440	46.57	83
Kaarru	-17.64	145.72	510	47.15	93
Charappa	-17.70	145.69	720	58.66	128
Charmillan	-17.71	145.52	890	34.64	87
Coochimbeerum	-17.68	145.50	1010	58.78	71
Cheelonga	-17.50	145.54	1100	50.09	72
Longlands	-17.45	145.48	1210	60.79	80

Map 1: Location of the 9 plots.



Sampling methods in the field

Sampling methods to determinate the rate of herbivory involved visual estimation of the percentage of leaf removed. In this study, we only considered phyllode-chewing to assess herbivory rates. The following scales was used: 0, ,<1, 1 – 5, 5 – 10, 10 – 15, 15 – 25, 25 – 50, 50 – 75, 75 – 100%, as done in Grubb et al. (2008). For each plant, we analysed 24 fully expanded leaves from a top, a mid-height and a bottom branch (8 leaves per branch). We sampled 75 random individuals from the understory in a shaded environment along a transect in each plot to obtain an outlook of the herbivory at the community level. We also sampled 10 individuals of the 2 following target species that we selected according to its presence throughout the altitudinal transect: *Mackinlaya confusa* and *Neolitsea delbata*. For both species, we only sampled individuals from shaded environments and human-reaching size. The objective was to characterize how a single species is affected by altitude and therefore temperature in terms of herbivory.

To estimate the exact number of leaves per plant and the number of individuals that had to be sampled, we used preliminary data to relate confidence intervals to sample size, which showed the minimum number of samples required to achieve the desired confidence interval of 95%.

We also calculated the percentage of damaged leaves (with any level of damage) based on the herbivory data from the field.

Sampling methods in the laboratory

We also studied leaf toughness for every sampled individual of the target species at every altitude, so that we could compare physiological treats of the species at different altitude as well as compare between species, as leaf toughness may be another factor influencing herbivory rates. To do so, we used two Chatillon Dial Tension Gauge penetrometers, calibrated against an electronic pan balance on April 2005. On of them was a model AG50 measuring 0-50g which read consistently 0.0 to 0.3 below balance value; and the other was a model AG150 measuring 0-150g which read consistently 0.3 to 0.6g below balance value. Both had only marginally detectable deviations from the "true" weight.

Statistical methods

We performed statistical tests to check the normality of the data, and in all the cases the analysis showed that the studied variables were normally distributed. Thus no data transformation was required. Linear regression analysis and Pearson correlation coefficients were used to quantify association between pairs of continuous variables. Multiple linear regression models were to model the relationship between the two response variables (Percentage of damaged leaves and mean leaf area loss) and explanatory variables, including mean annual temperature (MAT), basal area (BA) and plant diversity (H). Annual rainfall was not included in multiple regression models as it was highly correlated with mean annual temperature, potentially leading to multicollinearity and its associated problems (Gotelli & Ellison, 2004). All analyses were performed with the package SPSS and regressions were made with SPSS.

RESULTS

In general, we observe significant increases in both mean leaf area loss and percentage of damaged leaves with increasing temperature (Fig. 1 and 2).

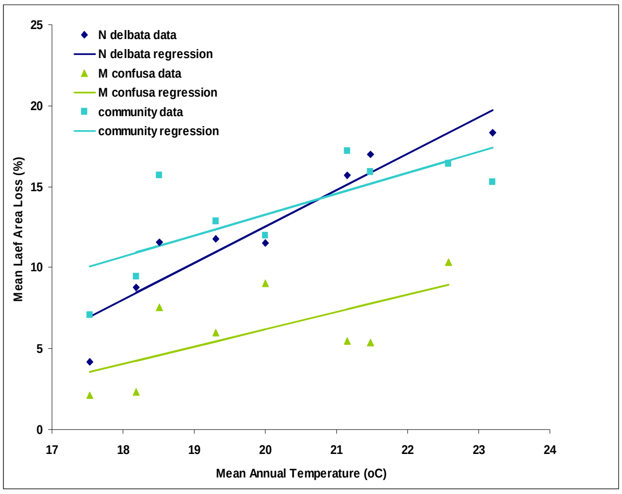


Fig 1: Mean leaf area loss and temperature regression for the community level, *N. dealbata* and *M. confusa*.

As we observe in Fig. 1, the mean leaf area loss for all samples goes from 2% to no more than 20%. In particular, for *Neolitsea dealbata* it increases from 4 to 17% (R^2= 0.87, p=0.0007), for *Mackinlaya confusa* it increases from 2 to 10% (R^2= 0.83, p=0.004), and for the community as a whole it ranges from 7 to 17% (R^2= 0.59, p= 0.015). In all cases the regressions are significant ($p<0.05$). Therefore, both for the overall community and for the two individual species leaf area loss is positively related to temperature.

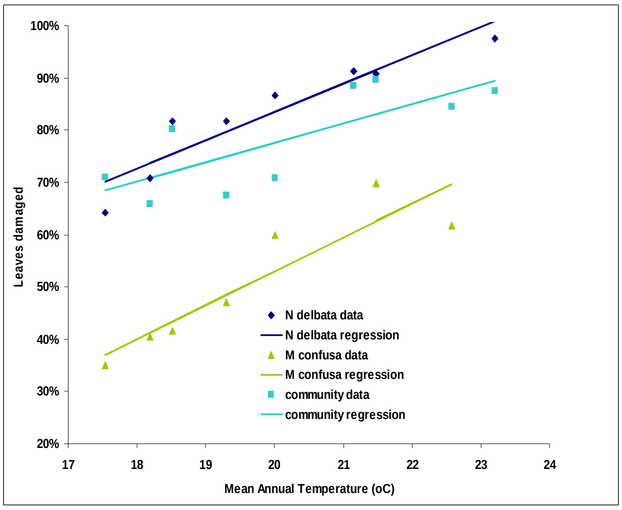


Fig. 2: Damaged leaves and temperature regression for the community level, *N. dealbata* and *M. confusa*.

The percentage of damaged leaves (Fig. 2) also increases as a function of temperature from approximately 65 to 85% for the community sampling (R^2 = 0.59, p=0.015). In this case, the trend is only marginally significant ($p>0.01$). For *N. dealbata*, the values of damaged leaves increase from 60 to 95% (R^2 = 0.87, p=0.0007), and shows the highest values registered in this study. Finally, *M. confusa* values also increase with temperature, from 35 to 70% (R^2 = 0.83, p=0.004). The regression is highly significant for the two species, showing a significant relationship between mean annual temperature and the percentage of damaged leaves.

		Annual Rainfall	BA	Site diversity Spp
%Loss Community	Pearson's Correlation	0,327	-0,462	0,531
	Sig. (bilateral)	0,39	0,21	0,142
	N	9	9	9
%Damaged Community	Pearson's Correlation	0,636	-0,292	0,464
	Sig. (bilateral)	0,066	0,447	0,208
	N	9	9	9
% Loss *M. confusa*	Pearson's Correlation	0,272	-0,236	0,345
	Sig. (bilateral)	0,514	0,574	0,402
	N	8	8	8
%Damaged *M. confusa*	Pearson's Correlation	0,699	-0,372	0,466
	Sig. (bilateral)	0,081	0,411	0,292
	N	7	7	7
% Loss *N. dealbata*	Pearson's Correlation	0,542	-0,622	0,654
	Sig. (bilateral)	0,165	0,1	0,079
	N	8	8	8
%Damaged *N. dealbata*	Pearson's Correlation	0,543	-0,535	0,595
	Sig. (bilateral)	0,164	0,172	0,12
	N	8	8	8

Table 2: Correlations between herbivory and damage parameters with climate and ecologic variables

A correlation analysis was performed (Table 2) in order to test whether mean leaf area loss and the percentage of damaged leaves were associated with other factors besides temperature. Studied explanatory variables included annual rainfall (AR), basal area (BA) and plant diversity (H), all available for all study plots. The tests were conducted at the community level as well as using data on the two sampled species. For the community level the percentage of leaf area loss showed no significant correlation with the AR, BA or Diversity. The damaged leaves variable showed no significant correlation with the other parameters.

For *M. confusa*, the Leaf Area Loss showed no significant correlation with any of the variables. We found a tendency within the AR correlation (R^2=0.70, p=0.081). No significant correlation was found with the BA or the Diversity.

For *N. dealbata*, both the Leaf Area Loss and the Damaged Leaves showed no significant correlations with the studied variables. In all cases, temperature was significant or showed a positive trend, but the effect of temperature has been already studied with the simple regressions, and it is not showed in this test.

Multiple regression analysis showed that, at the community level, leaf loss was mainly influenced by temperature, but the relationship was not statistically significant (Table 3). Leaf damage showed a better relationship (R^2=0.692, with a significant effect of temperature (p=0.04) (Table 4). Similar results were obtained in the models for *M. confusa* (R^2= 0.517 and R^2=0.978 for leaf loss [Table 5] and leaf damage [Table 6], respectively). Tables 7 and 8 show the results for *N. dealbata*, where the effect of temperature was always significant and the other variables were never significant. The effect of temperature was significant in all leaf damage cases ($p<0.05$), whereas basal area and diversity were never significant.

Variable	Standardized Coefficients	Degrees of freedom	p
	Beta		
MAT	0,741	3	0,197
BA	0,053	3	0,9
Site diversity Spp	0,054	3	0,899

Table 3: Multiple regression results for the mean leaf area loss at the community level.

Variables	Standardized Coefficients	Degrees of freedom	p
	Beta		
MAT	1,133	3	0,041
BA	0,411	3	0,273
Site diversity Spp	-0,131	3	0,712

Table 4: Multiple regression results for the damaged leaves at the community level.

Variables	Standardized Coefficients	Degrees of freedom	p
	Beta		
MAT	1,035	3	0,148
BA	0,374	3	0,469
Site diversity Spp	-0,2	3	0,693

Table 5: Multiple regression results for the mean leaf area loss of *M. confusa*

Variable	Standardized Coefficients	Degrees of freedom	p
	Beta		
MAT	1,412	3	0,002
BA	0,448	3	0,03
Site diversity Spp	-0,303	3	0,078

Table 6: Multiple regression results for the leaf damage of *M. confusa*

Variables	Standardized Coefficients	Degrees of freedom	p
	Beta		
MAT	0,9	3	0,038
BA	-0,002	3	0,993
Site diversity Spp	0,048	3	0,852

Table 7: Multiple regression results for the mean leaf area loss of *N. dealbata*

Variable	Standardized Coefficients	Degrees of freedom	p
	Beta		
MAT	1,091	3	0,017
BA	0,164	3	0,507
Site diversity Spp	-0,072	3	0,766

Table 8: Multiple regression results for the leaf damage of *N. dealbata*

The effect of leaf toughness on herbivory was studied on the two target species (not at the community level) using linear regression (Fig. 3 and 4). Our results showed no significant effect of toughness on either mean leaf area loss (Fig. 3) and percentage of damaged leaves (Fig. 4).

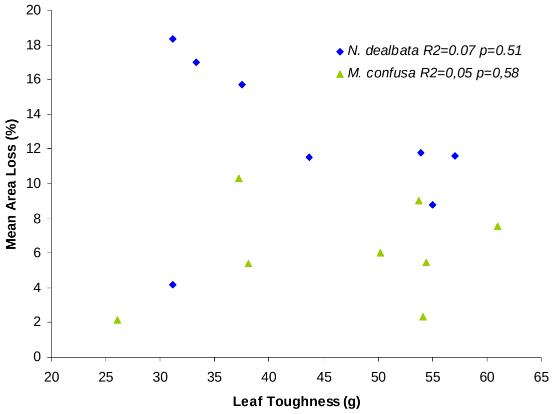


Fig. 3: Mean Leaf Area Loss and Leaf Toughness regression for *N. dealbata* and *M. confusa*.

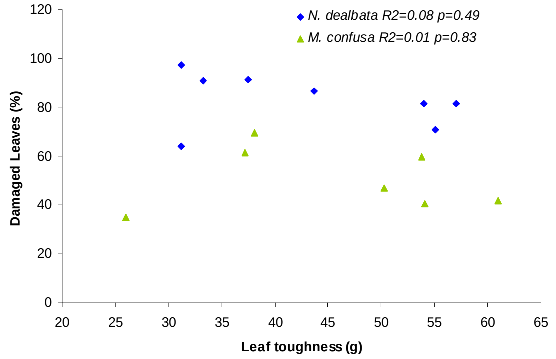


Fig. 4: Damaged Leaves and Leaf Toughness regression for *N. dealbata* and *M. confusa*.

DISCUSSION

The main observation made from this study is that the levels of insect damage (either leaf area removed or damaged leaves) increase along with temperature. At the community level, the observed rates of herbivory increased 1.3% $^{o}C^{-1}$ for the Mean Leaf Area Loss and 3.7% $^{o}C^{-1}$ for the Damaged Leaves. If we assume that current differences in temperature among sites are analogous to future temperature changes within a site, the previous values can be translated into predictions under climate change scenarios. Thus, if air temperature raises 3.5 degrees in the area, as predicted by some scenarios (Suppiah et al., 2009), the leaf area loss would increase

4.6% and the damaged leaves would increase 13%. These are expected results if we expect insect activity to increase along a positive temperature gradient (Bale, 2002), and knowing that increasing temperature shows higher herbivore attacks (Andrew, 2005; Coley, 1996). The obtained results are based on a temperature change along an altitudinal gradient, but given the prediction of increasing temperature in the future due to global warming, the present results are interpreted as an analogy of future global warming scenarios, so that they provide useful information for understanding the response of the ecosystem to the expected temperature changes. This is the main goal of a study of this kind and the same approach has been used by many other studies (Dunne et al. (2004).

The statistical tests that were performed suggest that the percentage of damaged leaves has a higher sensitivity to temperature than the mean leaf area loss (due to more significant results). Also, it is more influenced by temperature in the multiple regressions, so it might be a more suitable parameter to detect the effect of temperature changes than the amount of leaf area removed.

More specifically, the regressions from the two species show higher coefficients of determination (R^2) than the community ones. This is an expected result as the community level shows the response to herbivory from many plant species whereas the targes species focus on the selected species and results are more accurate. At the community level different species may respond in different ways, compensating each other.

We also observe how *M. confusa* has less damage level in both regression analyses. This could be due to stronger physical or chemical defences. According to our leaf toughness results, no correlation is found between insect attacks and leaf toughness, either within or between the two studied species, and therefore we suggest that *M. confusa* has stronger chemical defences than *N. dealbata*. This is also corroborated by the studies made by Hartley, (2007), who found that secondary chemical metabolites are more important against herbivory than physical defences.

Climate predictions for the next decades show that the global temperature of the world will increase up to 6 degrees by 2070 (IPCC, 2008), and up to 5 degrees in the Wet Tropics. This fact, combined with the results obtained in this study, leads to the conclusion that global warming is going to increase insect herbivory in the Wet Tropics rainforest. However, there are many factors that have not been taken into account in this study, such as changes in plant physiology and morphology under raising temperature, rainfall and CO_2 concentration changes due to climate change and unknown insect responses to these changes, to name a few. There are, nevertheless, several studies showing how in the past, during the Paleocene-Eocene Thermal Maximum, herbivory increased during a global warming episode (Currano, 2008; Wilf, 1999). More recently, De Lucía (2008) found that in the event of a combined increase of temperature and carbon dioxide, herbivore insects would increase their damage rate. Together with the present study, these results are alarming for the conservation of the Wet Tropics Area. It is thus possible that global warming increases herbivory in the Wet Tropics bioregion.

Similar studies carried out with more study sites for a same altitude and different methods would provide with more accurate data and would be very useful to compare. Moreover, wider and more accurate investigations on other factors affected by fast climate change and affecting rainforests and herbivory (such as insect response to climate change, other climate changing climate factors [Coley, 1999]), are needed in order to be able to fully understand the response of the Wet Tropics bioregion and preserve it.

Considering that NE Queensland rainforests are expected to be highly sensitive to global warming (Hilbert, 2001), the expected temperature increments could put a real threat to one of the most diverse and unique ecosystems of the world.

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