

# Ecology and evolution of the arborescent *Erica azorica* Hochst. (Ericaceae)\*

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**Abstract** The goal of this study is to evaluate the impact of insect herbivory on plant architecture of *Erica azorica* Hochst., an endemic species of the Laurisilva forests of Azorean islands. *Erica azorica* is an early successional species that can persist in mature Laurisilva, where trees are tall emergent individuals. The hypothesis tested is that the insect damage will modify whole plant architecture by decreasing the number of ramifications from the upper buds, the length of terminal shoots of a module, and thus the module structure. Plants were sampled in 1999 and 2000, during late (August-September) and early (July) summer, respectively. Three distinct populations were sampled in the Pico island: "Manhenha", which is a dominant early successional population; "Caiado", a population in an abandoned pasture on the highlands, in the "Caiado" lake; and "Mistério da Prainha", a population of emergent, 8 to 11 metres tall trees, in an old successional forest on recent volcanic soil. Ten plants were randomly sampled from each population. From each plant there 10 branch modules were collected from different positions and heights. Plant modules were counted for total number of branches, number of damaged branches, branch ramifications from the upper buds, and shoot growth. Previous insect damage could be readily identified, as it causes the re-growth of 3-4 twigs from the same meristematic point. Insect damage was then quantified by counting the number of destroyed and undamaged buds per module. Insect larvae found on modules were also quantified. Data were analysed using Nested ANOVA, Repeated Measures ANOVA, paired t-test, and multiple regressions, depending on objectives. The number of branch ramifications and shoot length were negatively affected by insect damage for all populations. However, the absolute figures showed that the coastal "Manhenha" population suffered less effect of damage on branch ramifications and shoot length than the "Caiado". The total number of branches in a branch module did not respond to insect damage, which may be related to the development of new branch module after a degree of shoot expansion. In other words, healthy branch modules may develop into a new module by expansion faster than a damaged module. Moreover, a high variability between plants, regardless of response to insect damage, was found. There is some evidence for plant tolerance to insect herbivory. The implications of this on plant performance, under a competitive scenario, and likely consequences of selective forces driven by the combination of herbivory and competition are discussed. The consequences for conservation and land use management are presented

**Key words:** *Erica azorica*, herbivory, architecture, arborescent.

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**Resumo** O objectivo do presente estudo consistiu em avaliar o impacto da herbivoria por insectos na arquitectura da urze *Erica azorica* Hochst, planta endémica da Laurisilva dos Açores. *Erica azorica* é uma planta com porte arbustivo e pioneira que consegue persistir nas florestas maduras de Laurisilva, onde pode atingir porte arbóreo tornando-se emergente no copado. Testa-se a hipótese de que a arquitectura da planta pode ser modificada através do dano provocado por insectos, dando-se esta alteração através do decréscimo do número de ramificações no botão terminal, alteração do comprimento dos ramos terminais de um módulo, e consequentemente alteração da estrutura do

módulo. Fez-se uma amostragem em 1999 (Agosto – Setembro) e 2000 (Julho) de três populações distintas na ilha do Pico: “Manhenha”, população pioneira; “Caiado”, população em pastagem abandonada nas margens da Lagoa do Caiado; e “Mistério da Prainha – Chão Verde”, uma população emergente, com árvores de 8 a 11 metros de altura numa floresta madura localizada numa corrente de lava recente. Foram amostradas ao acaso um total de 10 plantas por população, tendo-se colhido 10 módulos de ramos a diferentes alturas e posições dentro de cada planta. Em cada módulo contou-se o número de ramificações, número de ramificações danificadas, ramificações dos botões terminais, e crescimento dos ramos. O dano provocado pelos insectos foi identificado facilmente pois este provoca o reaparecimento de 3 a 4 novos ramos com origem no mesmo ponto meristemático. Deste modo, o dano provocado pelos insectos foi quantificado através da contagem do número de botões destruídos e de botões não danificados por módulo. Quantificou-se igualmente o número de larvas de insectos por módulo. Dependendo dos objectivos, a análise estatística dos dados fez-se utilizando ANOVA Hierárquica, “Repeated Measures ANOVA”, testes-t emparelhados e regressão múltipla. Observou-se que a herbivoria provocada pelas larvas de insectos afectou negativamente o número de ramificações e o comprimento dos ramos, sendo em termos absolutos menos afectada a população costeira da “Manhenha” e mais afectada a população do “Caiado”. Não se notou uma relação entre a herbivoria e número de ramificações num módulo de ramos o que pode estar relacionado com o facto de um módulo de ramos saudável se desenvolver mais rápido do que um módulo danificado, num novo módulo por expansão. Encontrou-se ainda uma certa variabilidade dentro de cada população e alguma evidência de tolerância da planta à herbivoria pelos insectos. Discute-se as implicações dos resultados em termos da resposta da planta à herbivoria em cenário de competição e impacto das forças da selecção natural. Finalmente, discute-se as consequências dos resultados em termos de conservação e gestão dos habitats.

**Palavra Chave:** *Erica azorica*, herbivoria, arquitectura, arborescência.

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## INTRODUCTION

Oceanic islands are well known by having arborescent plant species that belong to genera usually represented by herbaceous species in the mainland. A few examples are found in families such as Asteraceae, Apiaceae, Campanulaceae, Brassicaceae, Boraginaceae and Ericaceae (GIVNISH 1998). *Alsinidendron-Shidea* (Hawaii), *Echium* and *Argyranthemum* (Macronésia), *Lobelia* and *Dendrosenecio* (high altitude fields in East Africa, cited as a continental ancient island habitat), *Babcochia*, *Prenanthes*, *Sonchus*, *Sventenia*, *Taeckholmia*, *Ilex*, *Myrsine* and *Erica* (Macaronésia) are genera that have arborescent species only in

oceanic, or island-type habitats (GIVNISH 1998). A few largely discussed hypotheses to explain this fact are: 1) the survivorship of primitive species, now-a-days extinct in the continents (commonly refuted after molecular studies - mainly for Hawaiian cases) (see WAGNER & FUNK, 1995); 2) the longevity hypothesis (WALLACE 1878), that longer life span would be selected because it could increase the probability of reproductive success in a pollinator-poor habitat. In this case, plant height would be a consequence; 3) the competition hypothesis (DARWIN 1859; CARLQUIST 1974), that fast and unlimited growth could favour individuals under intense intraspecific competition. Little work has been done to understand the ecological mechanisms that

might be involved in the evolution and maintenance of arborescence in these species.

The goal of this study is to evaluate the impact of insect herbivory on plant architecture of *Erica azorica* Hochst., an endemic species of the Azorean islands, commonly found in native forests. Like many other insular species, *E. azorica* belongs to a genus of mainly herbaceous plants, but in the oceanic islands this species has woody trunks up to 5-6 m tall. For instance, *E. azorica* is an emergent species in old, well preserved forests, and it is able to resist the strong winds that follow the autumn storms. However, the species also covers extensive open areas after disturbance, being the dominant species in such habitats. In these conditions, a plant maintains a shrub architecture for many years. It seems unlikely that the shrub form could survive in a dense, mature Laurisilva community, due to intense competition for light and space with species such as *Juniperus brevifolia* (Seub.) Antoine, *Laurus azorica* (Seub.) J. Franco and *Ilex perado* Ait. ssp. *azorica* (Loes) Tutin (DIAS 1996). From preliminary observations in Pico island, several insect species were found attacking the branch buds: larvae of *Argyresthia atlanticella* Rebel (Lepidoptera, Yponomeutidae), *Cleora fortunata azorica* Pinker (Lepidoptera, Geometridae), an unidentified Geometridae species. An unidentified larva of Diptera is commonly found among damaged buds, but these insects were observed preying on lepidopteran larvae and not damaging the plant. All these herbivore species damage upper vegetative buds of the plants. The impact of these insects seems to affect greatly plant architecture, and eventually may even influence growth rates, and limit final height.

## MATERIAL AND METHODS

### SITES, SAMPLING DESIGN AND INSECTS\_

Plants were sampled during the expeditions of Project BALA (Biodiversity of Arthropods of the Laurisilva of the Azores; posted [http://www.nrel.colostate.edu/IBOY/europe\\_ap.html#BALA](http://www.nrel.colostate.edu/IBOY/europe_ap.html#BALA)) in 1999 and 2000, in the Pico island (Azores archipelago), during late (August-September) and early (July) summer, respectively. In 1999, two distinct populations were sampled: i) one on the coast, which is a dominant early successional population ("Manhenha"). Most of the plants from this population showed largely expanded shoots, suggesting fast, vertical growth; ii) the second population was found in an abandoned semi-natural pasture on the Pico's plateau (815 m above sea level), in the "Caiado" lake. Here, the plant individuals were low and rounded, apparently having slower branch growth. In 2000, the "Caiado" population was re-sampled and compared with individuals from Chão Verde forest at Natural Forest Reserve of "Mistério da Prainha" (525 m above sea level), hereafter referred to as the population of "Prainha". The latter is an old successional forest on recent volcanic soil, and individuals of *E. azorica* are mostly emergent, 8 to 11 metres tall trees.

Ten plant individuals were randomly sampled from each population. From each plant, 10 branch modules were collected from different positions and heights in the crowns. Plant modules were counted for total number of branches, number of damaged branches, branch ramifications from the upper buds, presence of flowers and shoot growth. In 1999, seasonal - identified by the light green colour - and total growth were measured. In 2000, since the plants were sampled in an early seasonal growth stage, only total ramification and total growth were measured. The population of "Prainha" showed

larger branch modules, with two ramification levels close to the upper buds, which were considered altogether. The buds were separated into damaged and undamaged by insects. Previous insect damage could be easily identified, as it causes the re-growth of 3 or 4 twigs from the same meristematic point. Insect damage was then quantified by counting the number of destroyed and preserved buds per module. Insect larvae found on modules were also quantified. A detailed list of the herbivorous insects feeding on *Erica azorica* is in preparation and will be published elsewhere.

## DATA ANALYSIS

A combination of different Analyses of Variance were used to test the hypothesis that insect herbivory modifies branch module architecture. Data from 1999 and 2000 were analysed separately. For 1999 data, firstly, an exploratory analysis was done for shoot growth and insect attack, comparing branch modules between populations, but regardless of plant individuals. Secondly, variances were compared between plant individuals nested within populations, and divided into damaged and undamaged, arbitrarily defined: in average less than 40 % of damaged buds per plant = undamaged plant; more than 40 % of damaged buds = damaged plant. Data exploratory analysis showed that a category of heavily attacked plants exists, and those plants had usually more than half of their buds attacked, therefore justifying the criteria used here. Finally, within plants, paired-sample t-tests were used to test the effect of insect attack, while removing variation among individuals, and therefore damaged branch modules were directly compared with undamaged modules.

In 2000, the sampling scheme enable precise within-plant comparisons. For each branch module, damaged and undamaged branches were randomly chosen, their ramification counted and the length of the tallest shoot measured. Repeated Measures ANOVA was

performed for the whole data set, with the branches nested within modules and plants, and compared according to damage, as repeated measures of each module. To test the hypothesis of different responses between populations, separate analyses were performed for "Caiado" and "M. Prainha".

The damage measured in 2000 was caused by the cumulative effect of insect herbivory in previous years. Therefore, the effects of the number of branches per module and the proportion of damaged branches per module (arcsine transformed) on the frequency of fruiting branches were tested by a Nested ANOVA. This analysis aimed to test whether previous damage could impact directly on fruit production in the following seasons. In addition, the effects of branch size and frequency of damage on present abundance of herbivore larvae were tested with a multiple regression, aiming to test whether insects could be choosing vigorous shoots, or, on the contrary, branches chemically more susceptible to attack (sensu PRICE 1991). Conversely, this same analysis allowed to test if damaged branches were avoided in the following year, which could suggest the existence of induced defences (see KARBAN & BALDWIN 1997). The whole data set has normal distribution, and is also sufficiently homocedastic.

## RESULTS

### CAIADO AND MANHENHA: 1999 DATA

Similar patterns of branch module development and insect attack were detected for both populations. The number of branches per module ( $F_{18,178} = 4.4, p < 0.001$ ), the number of ramifications in the upper buds ( $F_{18,178} = 3.6, p < 0.001$ ) and total shoot length ( $F_{18,178} = 3.8, p < 0.001$ ) varied significantly among individuals, regardless of populations (Multifactorial nested ANOVA). In addition, insect damage decreased significantly the overall number of terminal branches (Multifactorial nested ANOVA,  $F_{1,178}$

= 6.9,  $p < 0.01$ ), but not the total growth (Multifactorial nested ANOVA,  $F_{1,178} = 0.62$ ,  $p > 0.05$ ) or the seasonal shoot growth (Multifactorial nested ANOVA,  $F_{1,178} = 0.07$ ,  $p > 0.05$ ; Figure 1).

However, the absolute figures showed that the coastal "Manhenha" population suffered less damage effect on branch ramifications and shoot length than the "Caiado" (Multifactorial ANOVA:  $F_{1,196} = 39.3$ ,  $p < 0.001$ ;  $F_{1,196} = 15.3$ ,  $p < 0.001$ , respectively). This analysis also showed a significantly faster branch module development in "Manhenha" than in "Caiado", related to the insect damage factor (Multifactorial ANOVA: total branches,  $F_{1,196} = 4.2$ ,  $p < 0.05$ ; branch ramifications,  $F_{1,196} = 12.9$ ,  $p < 0.001$ ; shoot length,  $F_{1,196} = 25.5$ ,  $p < 0.001$ ).

Therefore, the plant trait which was mostly affected by insect attack was the number of ramifications from the upper branch, which was significantly smaller for damaged buds, in all analyses. On the other hand, the total number of branches in a branch module did not respond to insect damage ( $p > 0.05$ ), although there was a clear difference in the module format (extended vertically if undamaged, and expanded laterally if damaged).

The paired sample t-tests comparing modules with upper buds damaged against undamaged within each plant allowed the analysis of the direct effect of insect attack on module development. An upper branch grew less if its bud was previously damaged (mean = 5.5 cm) than when it was not damaged by insects (mean = 7.9 cm, t-test  $t_{16,0.05} = 2.2$ ,  $p < 0.05$ ). Likewise, the number of ramifications from the upper buds were significantly lower (mean = 5 shoots) when buds were damaged than when they were not (mean = 12 shoots, t-test  $t_{15,0.05} = 3.17$ ,  $p < 0.01$ ). For both damaged and undamaged branch modules, regardless plant individual or population, the number of shoots per upper bud and the length of the upper shoot were correlated. However, it is very clear that damaged modules had shorter and fewer shoots than unattacked ones (Figure 2).

## CAIADO AND PRAINHA: 2000 DATA

Branch ramification from upper buds varied significantly among plant individuals, in both "Caiado" and "Prainha" populations (Repeated Measures ANOVA:  $F_{8,77; 0.05} = 4.6$ ,  $p < 0.001$ ;  $F_{8,80; 0.05} = 2.63$ ,  $p < 0.05$ , respectively). The same pattern was found for shoot length (Repeated Measures ANOVA,  $F_{8,77; 0.05} = 8.24$ ,  $p < 0.001$ ;  $F_{8,80; 0.05} = 5.08$ ,  $p < 0.001$ , respectively). Comparisons between damaged and undamaged branches, nested within modules and plants, have shown that damaged branches consistently had fewer ramifications, regardless of populations (Repeated Measures ANOVA, Caiado:  $F_{1,77; 0.05} = 63.69$ ,  $p < 0.0001$ ; Prainha:  $F_{1,80; 0.05} = 119.9$ ,  $p < 0.0001$ ). Likewise, the length of shoots produced after damage were shorter than those growing from undamaged buds, in the population of "Caiado" (Repeated Measures ANOVA,  $F_{1,77; 0.05} = 9.16$ ,  $p < 0.05$ ). In the population of "Prainha", the pattern was not so clear (Repeated Measures ANOVA,  $F_{1,80; 0.05} = 1.9$ ,  $p > 0.05$ ). However, the interaction between the factors "shoot length" and "plant individuals" was significant (Repeated Measures ANOVA,  $F_{8,80; 0.05} = 3.6$ ,  $p < 0.001$ ), which was related to trees differing in their response. In other words, although several plants suffered no negative impact from bud damage on shoot growth, nearly half of them had reduced growth if the bud was previously damaged (Figure 3).

Fruiting was not affected by the size of branch module, neither by the amount of damage per module, despite significant variation in damage among individual trees (Table 1). On average, modules had 70 branches (s.d. = 25), and 50 % (s.d. = 20 %) of buds in a branch module were attacked, in both "Caiado" and "Prainha" (Table 1). Plants in "Caiado" had fruits on 20 % of branch modules compared to 50 % for plants in "Prainha". The size of branch modules and the proportion of damaged buds did not explain the abundance of insect larvae (multiple regression,  $F_{2,194; 0.05} = 1.9$ ,  $p > 0.05$ ). Therefore, no evidence

was found for insect branch module choice or induced defences.

## DISCUSSION

This study showed clearly that insect damage on vegetative buds can change plant architecture in important ways. By restricting the number of resprouting shoots and final shoot length, herbivory can affect growth rates, and potentially influence successful establishment, since *E. azorica* seems to be light limited (DIAS 1996). An interesting (but less obvious) pattern is that damaged and undamaged branch modules may have a similar number of branches, even though herbivory on buds decreases significantly the number of new shoots produced. It seems from this that the final architecture of a module will be constrained by something else. Therefore, a non-damaged module that produces many new branches may develop quickly into a new module, by vertical expansion of a set of upper branches. Eventually, resources from lower branches may be allocated to vertical growth of the new module, and thus result in a fast elevation of the crown. On the other hand, a damaged module may expand laterally, but does not generate a new module. Although the data do not show any direct influence of herbivory on lateral growth, re-growth of shoots after damage results in 3-5 short, but similar, shoots from the same starting point, which will fulfil a lateral space instead of causing vertical growth of the structure. RIBA (1998) found significant reduction in resprouting after intense manipulative crown damage in *Erica arborea*, which is consistent with the findings of the negative impact of insect herbivory on tree architecture of the congeneric *E. azorica* studied here.

The most relevant fact is that damaged plants do grow slower, and eventually very slow, depending on the intensity of the attack. The majority of insect damage occurred on individuals from the Caiado's population, which

is composed of low, rounded, shrub-type individuals. This population contrasts with the fast growing trees found in the "Manhenha" population. Similarly, they contrast with the tall, woody and emergent trees found in isolation in old and mature Laurisilva, such as that of population of "Prainha". As "Caiado" is an abandoned semi-natural pasture on a slope, there is little or no competition with other tree species. Even intraspecific competition is decreased due to the sparse and discontinuous distribution of plants. All three studied populations are located in the Northeast side of the Pico island, and thus major climatic differences are unlikely. Therefore, data indicate a significant negative impact of herbivory on plant architecture. However tolerance may exist (see below), re-growth can hardly result in significant compensation to damage for majority of plants, as observed for some other plant species evolved to respond to grazing (OBA et al. 2000, GADD et al. 2001). Although most of papers on herbivory impact are based on imposed herbivore damage, natural herbivory measure can provide unbiased conclusions considering the parameters tested here, but further conclusions on the herbivory impact on plant fitness needs experimental work (TIFFIN & INOUE 2000).

There may be ecological and evolutionary implications related to this kind of insect impact on plant architecture. The short shrub-type individuals will have difficulties to overcome the shadows that may appear when other species, like *Juniperus brevifolia*, *Laurus azorica* and *Ilex perado azorica*, colonise an abandoned or new habitat originally invaded by *E. azorica*. To consider that competitive pressure may favour fast growing individuals with wood structure agrees with the Darwin's hypothesis for evolution of arborescence in islands. Now-a-days this is one of the most accepted hypotheses, supported by studies using molecular-clocks and other genetic techniques (see WAGNER & FUNK, 1995). The hypothesis that oceanic islands preserved relict ancient trees of genera represented by herbs and

shrubs elsewhere has been proved unlikely for many species (GIVNISH 1998).

High variation in bud growth in response to insect damage in trees from the "Prainha" suggests the existence of plant tolerance to herbivory. On the other hand, no evidence was found of induced defences. In this population, genotypes strongly selected for optimisation in growth investments *versus* defence are likely, because it is composed only of emergent *Erica* trees, in a species rich and dense forest. In other words, all individuals of *E. azorica* in this population are successful genotypes in surviving the successional process, and may have been selected for herbivory resistance or tolerance, in case insect attack plays an important role in succession, by reducing competitive ability (see CONNELL & SLATYER 1977). Although growth rates were not measured for this population, the module sizes suggest that these trees have fast growth. MAZANCOURT & LOREAU (2000) have shown that selection of plant palatability in a scenario of grazing optimisation is not a straight forward process, but quite likely a phenomenon under the pressure of a diverse herbivore guild. MAURÍCIO et al. (1997) demonstrated that selection of tolerance and resistance are not mutually exclusive, and can drive selection towards maintenance of genotypes investing in both strategies under herbivory pressure. An important aspect related to this in the Azores is the fact that most of the abundant endemic herbivore species are generalists (see MELO, 2001). For instance, the most common larvae in the buds of *E. azorica* belongs to the Yponomeutidae species *Argyresthia atlanticella* Rebel, an endemic highly polymorphic lepidopteran larvae (SILVA et al, 1995). In this case, the presence of other more competitive tree species will be a smaller problem if these species are more palatable than *E. azorica*.

Plant resistance to the insect attacks will depend on the strength of the herbivory impact, which could be high considering the likely evolutionary scenario, where herbivory may

have been absent for a long time, thereby allowing reduced defences to evolve (VAN VUREN & BOWEN 1999). In conclusion, the ability to grow fast, to keep vigorous, may have been selected by a combination of herbivory and competitive forces. Therefore, if growth is kept fast, regardless investment in defence, which could occur on particularly rich soil types (HERMS & MATTSON 1992), and be related to compensatory ability (HOCHWENDER et al. 2000), resistance to insect herbivory should be positively selected. As pointed out by BELL et al. (1999), damage can affect directly branch construction by causing a reduction in bud numbers, and thus can strongly influence crown architecture. When the shape of the crown and its growth rates are relevant for plant competition, the effect of herbivory may reduce survivorship likelihood of an individual, thus its chance to reproduce. However, it will be necessary to test this hypothesis with a carefully designed manipulative study at Pico and other Azorean islands.

Indeed, further studies are necessary to support the concept of the evolutionary importance of such a pressure in selection and maintenance of arborescence in *E. azorica*. Namely, clipping experiments aiming to evaluate changes in plant shape and also reproductive success, after damage are important. Likewise, a larger sample scheme, aiming to replicate contrasting habitats, or forest types, and their effects on the pattern of insect damage is in course of analysis (Ribeiro et al., unpubl. data). Furthermore, it is not necessary that damage affects reproductive success, as damaged, low plants can invade and reproduce in open habitats. In this case, it may still be expected that emergent trees in mature Laurisilva forests will have a different population genetic structure compared with those in early successional habitats. Indeed, there may be a higher proportion of resistant individuals among emergent trees than in early successional populations (or in a population in Hardy-Weinberg equilibrium). Molecular techniques should be used to compare the genetic structure of populations. Many other

aspects of migration and population structure within and among islands of the Azorean archipelago can be developed, as this is a dominant and common species. It will also be important to know the level of herbivory that *E. azorica* suffers in nature in comparison with other Azorean endemic plants. Understanding the ecology of this yet unthreatened species could enlighten researchers and wildlife managers on the biological and evolutionary aspects mostly important for preservation of insular plant communities and processes, that have so many endangered species. Moreover, there is an urgent need to understand the population ecology of *E. azorica*, since the species readily invades agricultural lands, but is protected by law against cutting, thereby causing conflict of interests between production and conservation. The management plans that could reconcile farmer's interests with the maintenance of viable, genetically diverse, populations of *E. azorica* can only be made after a broader understanding of the species evolutionary ecology.

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Table 1 – Nested ANOVA results on the effect of the number of branches per module and the proportion of damaged branches per module on the frequency of fruiting branches, for the populations of “Caiado” and “Prainha” sampled in 2000 (fruiting was not affected by the size of branch module, neither by the amount of damage per module, despite of significant variation in damage among individual trees).

Source	SS	df	MS	F-test	p
Dependent variable: <u>Branch module size</u>					
<b>Within + residual</b>	64374.5	161	399.8		
<b>Fruiting within plant = error 2</b>	7581.3	17	445.96	1.12	0.34
<b>Population (vs error 1)</b>	720.5	1	720.5	0.28	0.6
<b>Plant within population = error 1 (vs error 2)</b>	46344.96	18	2574.7	5.8	0.0001
Dependent variable: <u>Proportion of damaged branches</u>					
<b>Within + residual</b>	4.74	161	0.03		
<b>Fruiting within plant = error 2</b>	0.27	17	0.02	0.53	0.93
<b>Population (vs error 1)</b>	0.27	1	0.07	0.47	0.50
<b>Plant within population = error 1 (vs error 2)</b>	2.58	18	0.14	9.14	0.0001

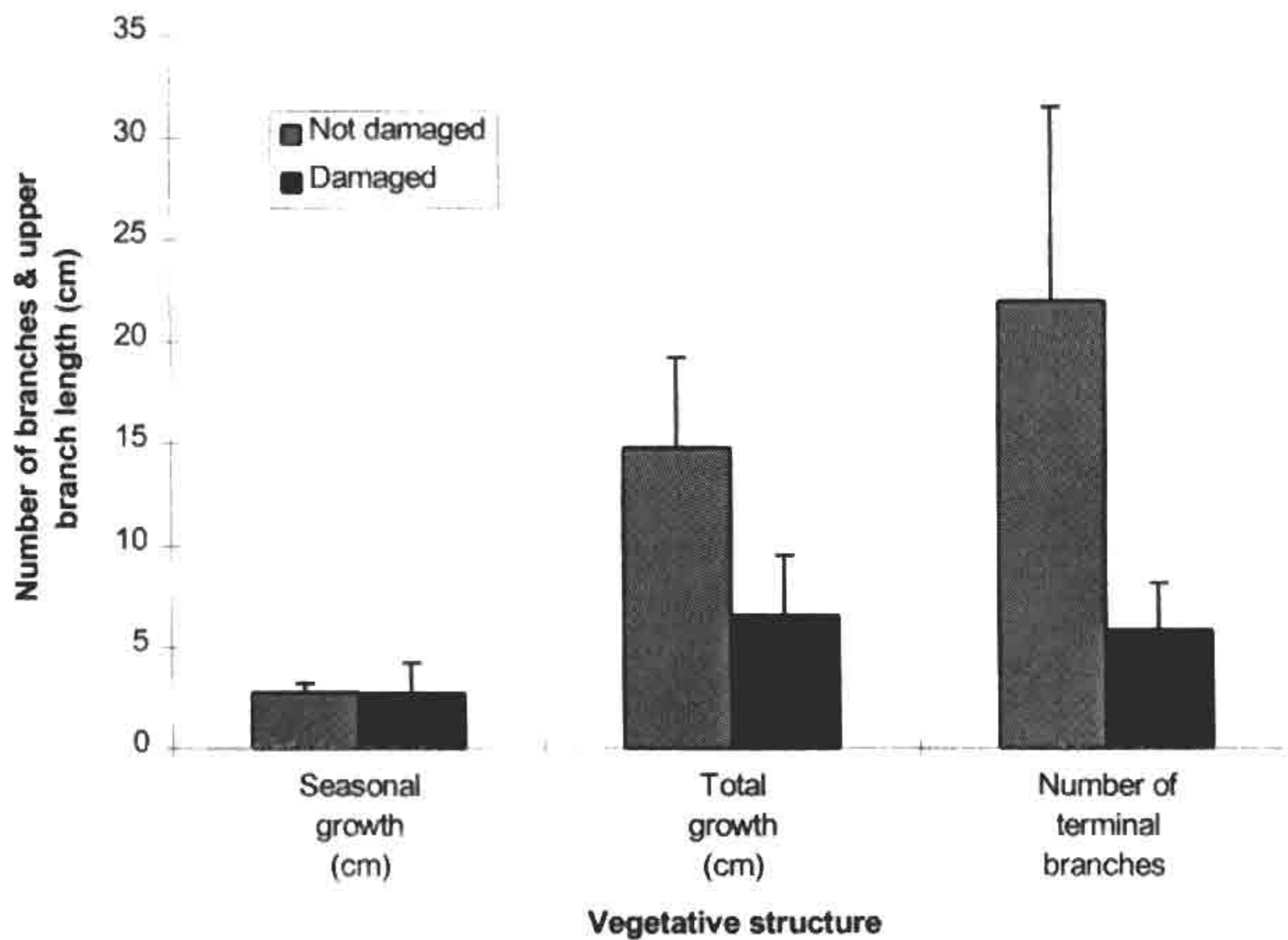


Figure 1 - Effect of insect damage on total shoot growth and number of branches from upper buds of *Erica azorica* in the Pico island, from the populations of Caiado and Manhonha (sampled in 1999), pooled together. Plants were defined as damaged when an average of more than 40 % of their branch modules were damaged.

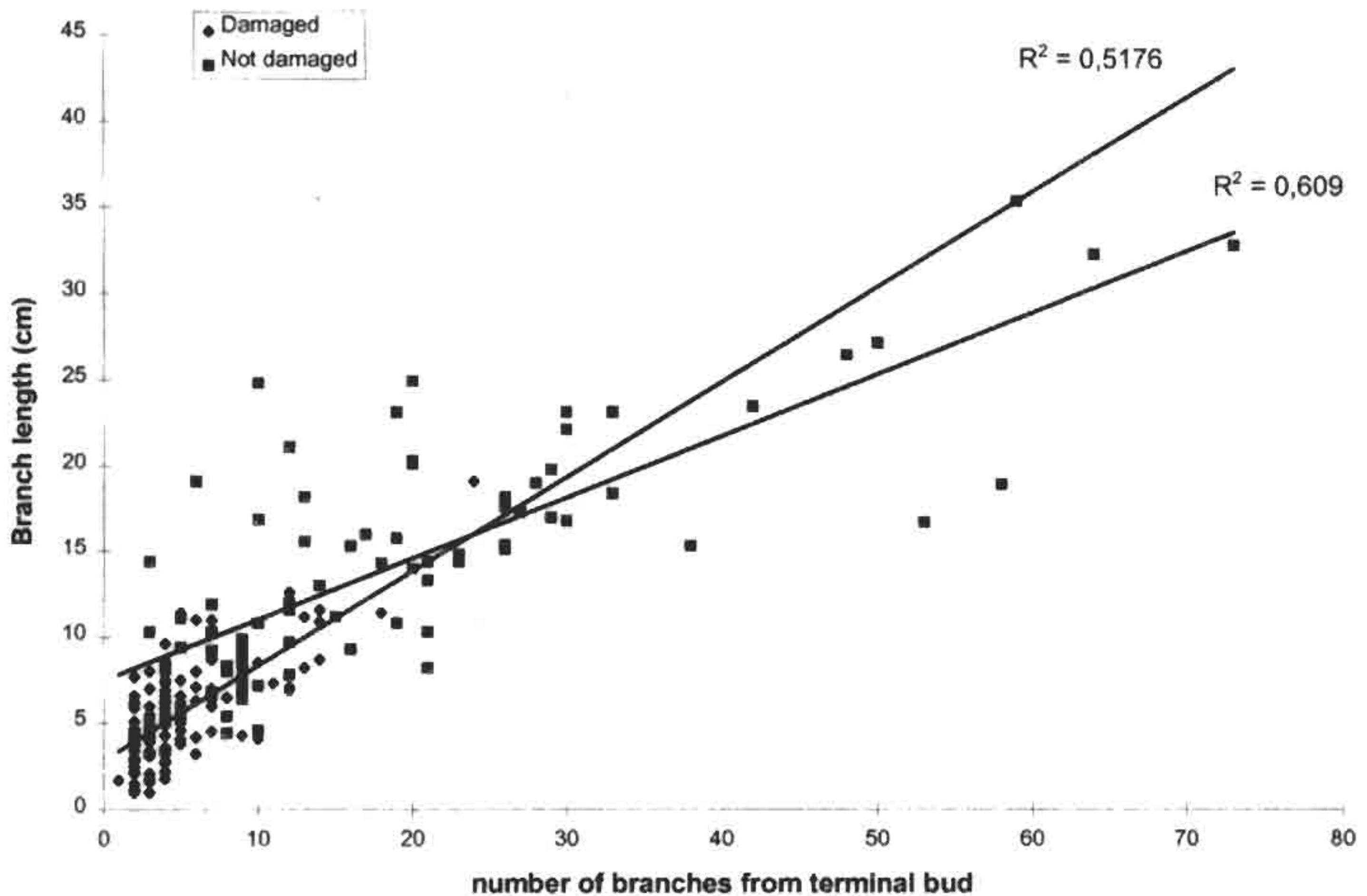


Figure 2 - Number of shoots from upper buds *versus* upper branch length of branch modules damaged and undamaged. Data shown for each individual branch module, regardless plant individual or population (Caiado and Manhonha, 1999 data).

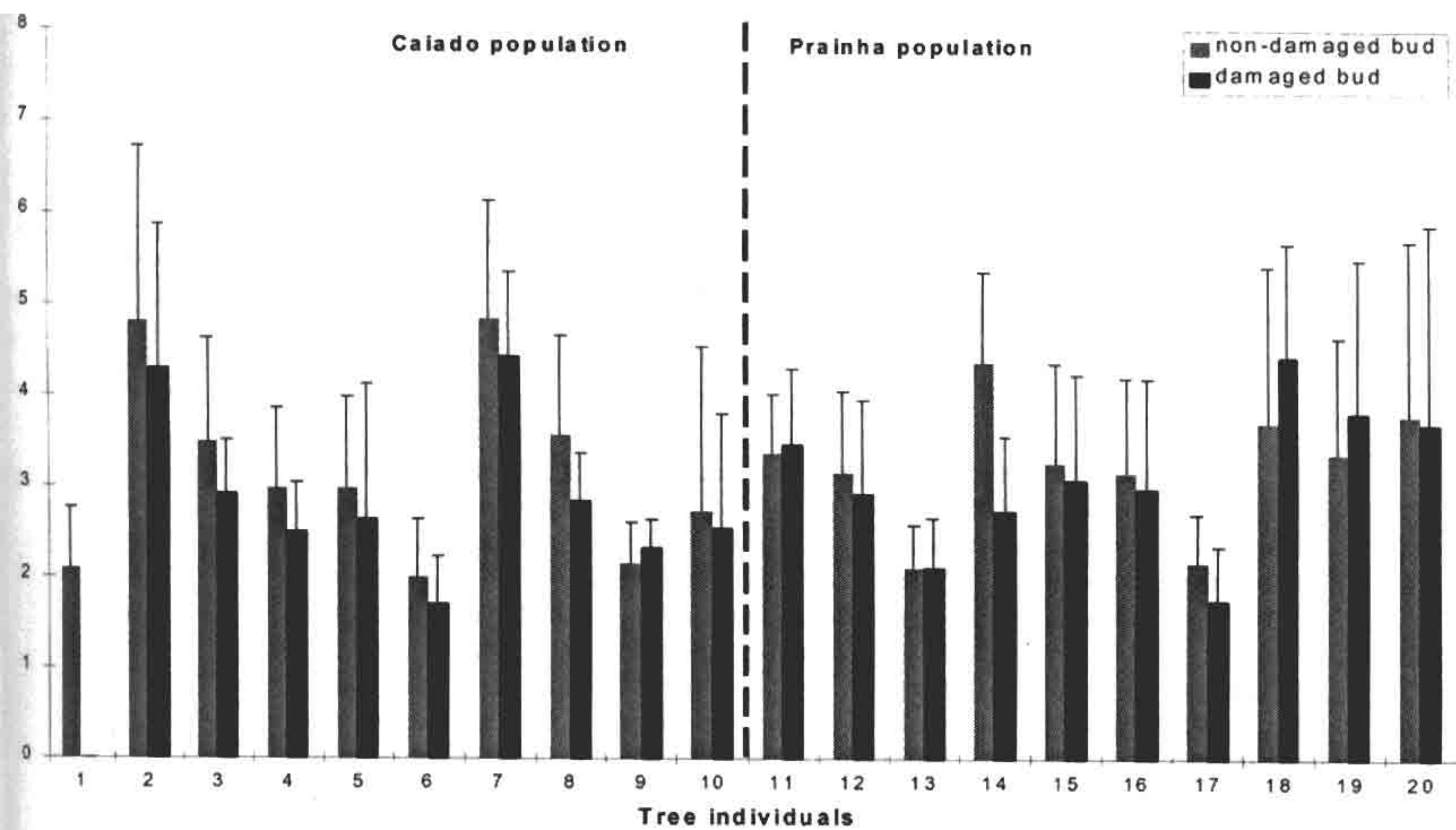


Figure 3 - Length (cm) of upper shoots (+ SE) from damaged and undamaged branches of 10 individual *E. azorica*, from the populations "Caiado" and "Prainha", sampled in 2000.