

THE EFFECTS OF RAMET DENSITY ON GROWTH AND BRANCHING OF *SALVINIA MOLESTA*

S.M. SOLANGAARACHCHI* and R.P.K. DUSHYANTHA

Department of Botany, University of Kelaniya, Kelaniya.

(Received: 21 August 1995; accepted: 07 June 1996)

Abstract: Single ramets of the tropical, floating, freshwater, aquatic weed, *Salvinia molesta* at its tertiary stage were grown at initial densities of 16 plants, 80 plants and 160 plants per square meter, in a pond. Growth parameters were measured for each plant separately after 6 wks. Results showed that the number of nodes and leaves, the mean internodal length, the length of whole stolons, the dry weight of plants, the number of branches and the percentage branching decreased significantly ($p < 0.05$) with increasing initial density of ramets.

Key words: Ramets, *Salvinia molesta*.

INTRODUCTION

Plants are modular, in that they develop through iteration of morphological units termed modules. The iteration of these units, the leaf with its axillary bud and associated internode forms a branching structure,¹ which depends on the branch angle, the internode lengths and the dynamics of the birth and death of meristems; and hence the arrangement of modules in space. Branching determines the fitness of an organism which depends on the number of descendants that a genet contributes to future generations. Although the branching pattern is genetically determined, its rules may change continually depending on the availability of resources. The response of modules to local environment was demonstrated by Noble,² who provided different local nutrient conditions to each module of a single rhizome of *Carex arenaria* L. Furthermore, light quality (reduced red to far-red ratio) and quantity (reduced light intensity) reduced the branching of *Trifolium repens* L.³ Factors such as soil moisture, nutrient supply and the season also affect the branching of *T. repens*.⁴

The presence of both intraspecific and interspecific neighbours changes its local environment (e.g. availability of resources), affecting the growth of individuals in a population both at genet level and modular level. Thus higher densities (intra-specific neighbour effects) may increase the risk of mortality of genets,⁵ and on the other hand, they may alter birth and death rates of their modules such as leaves, branches, flowers, fruits, rootlets etc.

* Corresponding author.

The response of plants to the density stress at modular level is expressed in the reduction in size frequently measured in terms of biomass.⁵⁻⁹ Reduced size however is mainly due to the effects at modular level and hence due to reduced branching.^{7,10,11} In clonal plants, density stress may influence modules more than genets.

The clonally spreading, floating aquatic fern *Salvinia molesta* Mitchell is a problematic weed in tropical fresh water bodies. The plant is sterile¹² and therefore population increase depends on vegetative growth and branching. The plant develops branches from lateral buds, which arise in leaf axils on alternate sides of the stolon at successive nodes. Although there are three lateral buds in each axil it is the first rank bud that develops into branches under natural conditions, and the second and third rank buds develop in high nutrient conditions.¹³

The weed is being biologically controlled by a weevil *Cyrtobagous salviniae* Calder and Sands.¹⁴ In monitoring control programmes it is essential to know the behaviour of individuals and their parts under different environmental conditions such as availability of resources. The behaviour of individuals may then be interpreted in the context of the population. As the plant's fitness depends on vegetative propagation, studies on the growth and branching are of great importance. Reduced growth and branching due to the effects of damage to leaves and roots and increased branching due to severance of stolons have been reported.¹⁵ The effect of density of plants on its morphological plasticity has also been studied.¹⁶ In thick growing mats of *S. molesta* (i.e. at the tertiary stage) density stress is unavoidable.

The results of experiments designed to study the effect of initial density of ramets (leaf pair with its root and axillary buds) at their tertiary stage¹⁷ on growth and branching of *S. molesta* are reported here.

METHODS AND MATERIALS

The pond of 5x3x1 m in the botanical garden of the University of Kelaniya, was cleaned and layered with mud to 25 cm brought from a place where *S. molesta* grew densely, to which pond water was added upto 90 cm in height. This level was maintained throughout the experiment by adding pond water. Eighteen wooden frames (quadrats) of 25x25 cm were placed afloat in the tank. The rootlets of all treatments share the same growth medium, although their above-water modules are partitioned by having the wooden frames.

Uniform (in age and size) single node cuttings (ramets) were selected from a healthy clone of *S. molesta* at its tertiary stage, and were used for different treatments. The following treatments were allocated to each frame using six

replicate quadrats for each treatment. The lay-out of the experiment was a completely randomized design:

Treatment 1 (T1) - Control - Density - one ramet per quadrat (16 plants/m²)
Treatment 2 (T2) - Density - Five ramets per quadrat (80 plants/m²)
Treatment 3 (T3) - Density - Ten ramets per quadrat (160 plants/m²)
Temperature of the water was $28 \pm 1^{\circ}\text{C}$ during this period.

After six weeks of growth each individual plant was destructively harvested and number of nodes and leaves on main and primary stolons (stolons arising from main stolon), number of branches on the main stolon, length of main and primary stolons, and the mean internodal length of the main stolon were measured. Five randomly selected plants from T3 treatment quadrats were taken for measurements. Then the plants were washed carefully and the leaves, roots and stolons were separated in each plant and were placed in separate paper bags and oven dried at 70°C , and the final constant weights were recorded. The percentage branching was then calculated.

The analysis of variance was carried out on the MINITAB data analysis package on a Commodore PC 10 III. Multiple comparison tests were carried out for the comparison between three treatments using Sheffe's method.¹⁸ Each experiment was carried out three times and the results were similar. Hence the results of the third experiment are reported here.

RESULTS

Table 1 shows the overall values for the parameters for each individual in each treatment. The number of nodes, leaves, the length of stolons, the internode length, the number of branches, percentage branching and dry weights of leaves, roots and stolons were highest in the control, and decreased with increasing density of individuals. The number of nodes on the main stolon of each individual plant decreased significantly ($p < 0.05$) by 12% and 18% in the intermediate (T2) and in the highest (T3) density treatments respectively. The effect on the number of nodes on primary stolons was greater than that on main stolons. The highest number of nodes was found in the control treatment, whilst it was reduced by 69% and 98% in T2 and T3 treatments respectively. The number of leaves on the main stolons were reduced to 89% and 83% of the control in T2 and T3 treatments respectively whilst the reductions were 68% and 98% in T2 and T3 treatments respectively on primary stolons.

Control plants had the longest main stolons, and in the other two density treatments, the length decreased by 18% and 25% respectively. The effect was greater in the primary stolons than that found in the main stolon. These reductions were 67% and 98% in T2 and T3 treatments respectively. The mean internode length was also significantly ($p < 0.05$) decreased by 30% and 35% of

the control in the intermediate and highest densities respectively. Number of branches on the main stolon was the highest in the control plants and it has reduced by 56% and 83% in the T2 and T3 treatments respectively.

Table 1: The effect of density on branching of *S. molesta*

Variable	Treatments		
	T1	T2	T3
<i>Number of nodes</i>			
Main stolon	12.83 ± 0.30a	11.23 ± 0.08b	10.50 ± 0.06c
Primary stolons	24.00 ± 0.96a	07.50 ± 0.32b	00.50 ± 0.02c
<i>Number of leaves</i>			
Main stolon	25.33 ± 0.61a	22.46 ± 0.14b	21.06 ± 0.12c
Primary stolon	47.33 ± 2.02a	15.10 ± 0.64b	01.00 ± 0.05c
<i>Length</i>			
Main stolon (cm)	11.16 ± 0.21a	09.15 ± 0.16a	08.32 ± 0.16b
Primary stolons (cm)	17.30 ± 1.12a	05.76 ± 0.29b	00.37 ± 0.03c
<i>Mean Internode length (cm)</i>	00.91 ± 0.03a	00.64 ± 0.01b	00.59 ± 0.00bc
<i>Number of branches</i>			
Main stolon	03.16 ± 0.31a	01.40 ± 0.04b	00.55 ± 0.02c
Percentage branching	25.28 ± 2.21a	12.51 ± 0.38b	05.48 ± 0.22c
<i>Dry weight (g)</i>			
Leaves	00.28 ± 0.02a	00.21 ± 0.00b	00.16 ± 0.00c
Roots	00.29 ± 0.02a	00.19 ± 0.00b	00.14 ± 0.00c
Stolons	00.04 ± 0.00a	00.02 ± 0.00a	00.20 ± 0.00a

Each value is an overall mean for six replicate quadrats. T1 - one ramet per quadrat (control), T2 - five ramets per quadrat, T3 - ten ramets per quadrat. Mean ± se sharing the same letter within each row do not differ significantly ($p > 0.05$).

The highest percentage branching was found in the control plants and there was a gradual yet, significant ($p < 0.05$) decrease with increasing density of individuals, and the reductions were 50% and 78% in T2 and T3 treatments respectively. The density treatments affected the dry weights of leaves and roots significantly ($p < 0.05$). The dry weights were highest in the control treatment, whilst there was a gradual decrease with increasing density. Dry weights of leaves reduced to 75% and 57%, roots reduced to 66% and 48% whilst stolons reduced to 50% in both T2 and T3 treatments.

DISCUSSION

The results show that plants grown at higher densities were less branched and smaller in size. The observed results are supported by similar observations made by various authors for erect plants with single stems or stages of plants with single stems, e.g. *Helianthus annuus* L.,¹¹ *Spergula arvensis* L.,¹⁰ *Trifolium subterraneum* L.¹⁹ Clonally spreading plants also have shown less branching at high densities, e.g. at high densities the rate of tiller formation decreased in *Lolium perenne* L.⁹ Similar results have been reported for *Trifolium repens*.^{20,21} Solangaarachchi and Harper²² have also shown that in *T. repens* plants, when grown close to each other branching decreased on interfering sides. At higher densities, plants and their parts compete for the same limited resources (nutrients, water, light and space) available in their immediate environment and this probably influenced the growth and branching of individual plants of *S. molesta* at higher densities.

At higher densities plants with erect stems elongate their stems (via internode length) which helps keep the leaves exposed to better light. In the present study mean internode length and the length of primary but not main stolons decreased significantly at higher densities. This is probably because stolons grow horizontally and an increase in their extension rate does not place the leaves higher in the canopy. Branching or their further development can continue until all the space is occupied by Resource Depletion Zones (RDZs).²³ Thus branching may change according to the availability of resources. Similar results have been found for fungal colonies (J.L. Harper personal communication).

The nutrient content in water is probably uniformly distributed and therefore even at higher densities, nutrient limitation may not be a significant factor. Thus in the present experiment reduced branching of each individual at higher densities could have been due to the availability of less space, which could have influenced the light quantity as well as light quality. At higher densities bud sites are naturally shaded by leaves of individuals,²⁴ whereas at lower densities the natural shading occurs to a less extent. Thus bud sites may not have been well exposed to light at higher densities, and further development of them may have been inhibited, e.g. reduced growth and branching at low light intensities have been reported for *Trifolium repens*.^{3,25}

References

1. Harper J. L. (1981). The concept of population in modular organisms. In: *Theoretical ecology*, (Ed. R. M. May), pp. 53-77. Blackwell Scientific publications.
2. Noble J.C. (1976). *The population biology of rhizomatous plants*. Ph.D. Thesis, University of Wales, U.K.
3. Solangaarachchi S.M. & Harper J.L. (1987). The effect of canopy filtered light on the growth of white clover (*Trifolium repens*). *Oecologia* (Berlin) **72**: 372-378.
4. Chapman D.F. (1983). Growth and demography of *Trifolium repens* stolon in grazed pastures. *Journal of Applied Ecology* **20**: 597-608.
5. Yoda K., Kira T., Ogawa H. & Hozumi K. (1963). Self thinning in overcrowded pure stands under cultivated and natural conditions. *Journal of Biology Osaka City University* **14**: 107-129.
6. Clatworthy J.N. (1960). *Studies on the nature of competition between closely related species*. D. Phil. Thesis, University of Oxford.
7. Harper J.L. (1961). Approaches to the study of plant competition. In: *Mechanisms in biological competition* (Ed. F.L. Mithorpe). *Proceedings of the Symposium of the Society of Experimental Biology* **15**: 1-39.
8. Ross M.A. & Harper J.L. (1972). Occupation of biological space during seedling establishment. *Journal of Ecology* **66**: 77-88.
9. Kays S. & Harper J.L. (1974). The regulation of plant and tiller density in a grass-sward. *Journal of Ecology* **62**: 97-105.
10. New J. (1961). Biological flora of the British Isles: *Spergula arvensis*. *Journal of Ecology* **49**: 205-215.
11. Kobayashi S. (1975). Growth analysis of plants as an assemblage of internodal segments: a case of sunflower plants in pure stand. *Japanese Journal of Ecology* **25**: 61-70.
12. Loyal D.S. & Grewal R.K. (1966). Cytological study on sterility in *Salvinia auriculata* Aublet with a bearing on its reproductive mechanism. *Cytologia* **31**: 330-338.

13. Room P.M. (1984). Plant architecture and how biological control agents affect the dynamics of weeds. *Proceedings of the VIth International Symposium of Biological Control of Weeds*. (Ed. E.S. Delfosse), pp. 89-102. Vancouver, Canada.
14. Room P.M., Harley K.L.S., Forno I.W. & Sanda D.P. (1981). Successful biological control of the floating weed *Salvinia*. *Nature (Lond.)* **294**: 78-80.
15. Solangaarachchi S.M. & Dushyantha R.P.K. (1991). Growth and branching of damaged *Salvinia molesta*. *Journal of National Science Council of Sri Lanka* **22**(3): 271-278.
16. Solangaarachchi S.M. & Hapuarachchi H.T. (1995). Intraspecific neighbour effects on the growth and morphological plasticity of *Salvinia molesta*. *Journal of National Science Council of Sri Lanka* **23**(1): 31-38.
17. Mitchell D.S. (1970). *Autoecological studies of Salvinia auriculata Aubl.* Ph.D. Thesis, University of London.
18. Zar J.H. (1984). *Biostatistical analysis*. 2nd edition. Prentice-Hall International Inc., London.
19. Donald C.M. (1951). Competition among pasture plants. I. Intra-specific competition among annual pasture plants. *Australian Journal of Agricultural Research* **2**: 355-376.
20. Erith A.G. (1924). *White clover (Trifolium repens L.)*. A monograph. Duckworth, London.
21. Harvey H.J. (1979). *The regulation of vegetative reproduction*. Ph.D. Thesis, University of Wales.
22. Solangaarachchi S.M. & Harper J.L. (1989). The growth and asymmetry of neighbouring plants of white clover (*Trifolium repens L.*) *Oecologia* **78**: 208-213.
23. Begon M., Harper J.L. & Townsend C.R. (1990). *Ecology*. 2nd edition. Blackwell Scientific Publications, London.
24. Trautner J.L. & Gibson P.B. (1966). Fate of white clover axillary buds at five intensities of sun-light. *Agronomy Journal* **58**: 557-559.
25. Black J.N. (1960). The significance of petiole length, leaf area and light interception in competition between strains of subterranean clover (*Trifolium subterraneum L.*) growth in swards. *Australian Journal of Agricultural Research* **11**: 277-291.