Influence of Physiological Integration on Survivorship and Water Relations in a Clonal Herb

Robyne R. Lau; Donald R. Young

Ecology, Vol. 69, No. 1 (Feb., 1988), 215-219.

Ecology, 69(1), 1988, pp. 215–219

INFLUENCE OF PHYSIOLOGICAL INTEGRATION ON SURVIVORSHIP AND WATER RELATIONS IN A CLONAL HERB[1]

ROBYNE R. LAU AND DONALD R. YOUNG[2]
Department of Biology, Virginia Commonwealth University, Richmond, Virginia 23284 USA

Abstract. To determine the extent of physiological integration in the clonal herb *Lycopodium flabelliforme,* the survivorship and water relations of severed and connected ramets were compared. In the field, severed ramets experienced 50% greater mortality than intact ramets. In greenhouse experiments, the xylem pressure potentials of severed ramets exposed to 200 $\mu mol \cdot m^{-2} \cdot s^{-1}$ of photosynthetically active radiation were as much as 1.3 MPa lower than the xylem pressure potentials of intact illuminated ramets connected to shaded ramets.

Thus, a water potential gradient develops within the xylem and facilitates water movement between shaded ramets and connected, illuminated ramets. Measurements of root distribution and capacitance supported this conclusion. Although each ramet did not necessarily have an associated root, water storage was greatest in roots and in ramet crowns, suggesting that irradiated ramets lacking nearby roots must rely on other ramets for water. Physiological integration of *L. flabelliforme* ramets facilitates water movement in the xylem, which may moderate the effects of environmental variability on ramet water potential.

Key words: clonal growth; forest herb; Lycopodium flabelliforme; *physiological integration; ramet; resource heterogeneity; translocation; water movement.*

INTRODUCTION

According to Pitelka and Ashmun (1986) clonal integration may provide adaptive advantages for reproduction and survival in environments with patchy resources. In the forest understory irradiance is a resource variable in time and space (Hutchinson and Matt 1977). This variability results in limited carbon assimilation for understory species and should favor integration. Carbon translocation between ramets of clonal plants may enhance survivorship in densely shaded microsites that have an abundance of other resources (Schellner et al. 1982). The ability of clonal species to translocate resources may favorably affect the life history traits of genets by enhancing vegetation propagation and sexual reproductive effort (Ryle and Powell 1972). The environmental variability in the forest understory has stimulated several studies on the adaptive significance of clonal integration in this environment (Pitelka et al. 1980, Ashmun et al. 1982, Flanagan and Moser 1985).

The examination of physiological integration has centered primarily on the phloem transfer of carbon between ramets (Marshall and Sagar 1968, Ginzo and Lovell 1973, Ashmun et al. 1982; Hartnett and Bazzaz 1983, Flanagan and Moser 1985). Far fewer studies have examined water transport (Raphael and Nobel 1986), although nutrient translocation studies have indirectly illustrated xylem integration patterns (Pitelka and Ashmun 1986). The studies directed specifically at xylem integration found differences in water transport patterns based on the degree of environmental stress (Quereshi and Spanner 1971, Tietema and van der Aa 1981, Salzman and Parker 1985, Alpert and Mooney 1986). However, the paucity of research on clonal water relations leaves the subject poorly understood (Pitelka and Ashmun 1986). Indeed, no studies have focused on water relations in regard to the clonal growth and survivorship of herbaceous species within the forest understory. Clonal understory herbs represent an excellent system for examining the adaptive significance of xylem integration because of the heterogeneous light environment and the short interramet distance for water movement along the rhizome. The purpose of the present study was to determine the extent of xylem integration within the understory clonal herb *Lycopodium flabelliforme.* Specifically, the influence of interramet rhizomatous connections on ramet survivorship and xylem pressure potential were examined in field and greenhouse experiments.

METHODS

Lycopodium flabelliforme (Fernald) Blanchard of the Lycopodiaceae is a perennial, evergreen herb with aboveground ramets connected by a creeping rhizome (Harvill et al. 1979). At the field site (37°25′ N, 77°32′ W), located ≈10 km south of Richmond, Virginia, *L. flabelliforme* was the dominant understory herb. The overstory, a mature, mixed deciduous forest (1158 trees/ha), was dominated by *Quercus alba, Liquidambar styraciflua, Liriodendron tulipifera,* and *Carya glabra.*

Several morphological characteristics of *Lycopo-*

---

[1] Manuscript received 16 February 1987; revised 18 May 1987; accepted 23 May 1987.

[2] Address reprint requests to D. R. Young.

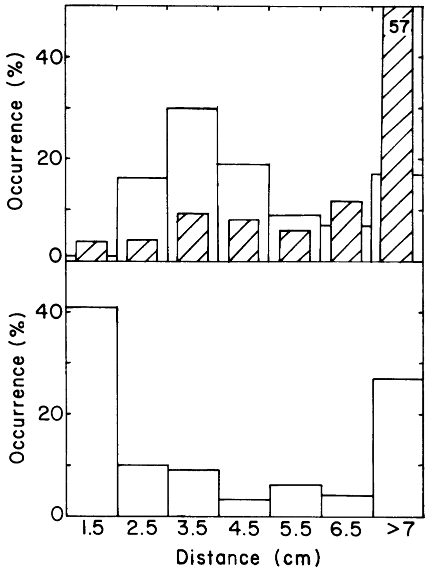

FIG. 1. Frequency distributions of interramet (open bars) and interroot (hatched bars) distances (top) and distance from root to nearest ramet (bottom) for genets of *Lycopodium flabelliforme.*

dium flabelliforme were measured in order to relate possible xylem pressure potential patterns to root distribution. These included interroot, interramet, and root-to-nearest-ramet distances ($N = 200$) of 20 randomly chosen, excavated genets. The significance of clonal growth to survivorship was determined in a field study that involved severing randomly selected ramets ($N = 250$) in five different patches and monitoring survivorship from May to October 1986. A month prior to the first measurements, the rhizome on both ends of ramets was severed with minimal disturbance to the plants and to the environment. For comparison, randomly selected intact ramets ($N = 250$) in five other patches adjacent to the severed treatments were monitored for the same period. In addition, the survivorship of severed ramets in a relatively open microsite ($N = 50$) and in a shaded microsite ($N = 50$) was compared between August and October 1986.

To examine the significance of clonal growth to water relations of *L. flabelliforme,* xylem pressure potentials of randomly chosen connected and severed ramets (six each) in the field were measured with a pressure chamber (PMS Instrument Company, model 650) at 2-h intervals throughout the day at ≈2-wk intervals from May through October of 1986. After *L. flabelliforme* clones were collected at the field site, water storage within the plants was also examined. The collected plants were rehydrated for a 12-h period, after which they were divided into four portions: root; underground rhizome; upright, aboveground stem; and crown, which consisted of forking branchlets. Capacitance (i.e., water storage) was determined for each

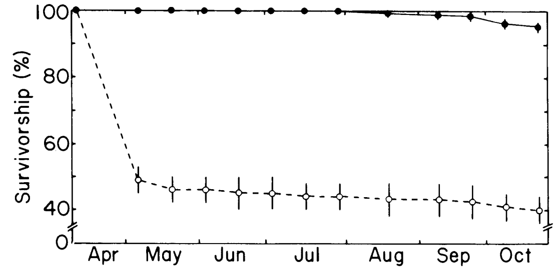

FIG. 2. Survivorship of severed (○) and intact (●) ramets of *Lycopodium flabelliforme.* Vertical bars denote ±1 SE for the means.

portion using the pressure chamber and the procedure described by Nobel and Jordon (1983).

The degree of water movement within clones of *L. flabelliforme* was examined in a greenhouse by monitoring the variation in the xylem pressure potential of ramets. Genets (each consisting of 18–27 ramets) were collected at the field site and allowed 1 mo to acclimate to the greenhouse environment, after which a number of the ramets were severed and allowed another month to acclimate before beginning the experiment. To minimize the effect of transpiration flux on xylem pressure potentials, all plants were covered with opaque plastic bags for the 24-h period preceding measurements. The experiment was performed in triplicate on sets of 18–24 ramets and consisted of the following three treatments: (1) severed ramet pairs exposed to 200 $\mu mol \cdot m^{-2} \cdot s^{-1}$ of photosynthetically active radiation (PAR, 0.4–0.7 μm), (2) an intact genet with one half exposed to 200 $\mu mol \cdot m^{-2} \cdot s^{-1}$ of PAR and the remaining half bagged and kept in the dark, and (3) a control genet, bagged and kept in the dark.

Every 10–15 min for a 120-min period, xylem pressure potentials were measured with the pressure chamber for illuminated severed, illuminated intact, dark intact, and control ramets. The position on the rhizome of the shaded ramets relative to the illuminated ramets (i.e., basipetal or acropetal) and the distance between the shaded, intact ramets and the nearest illuminated ramet were also noted.

Statistical analysis of the data included a Chi-square

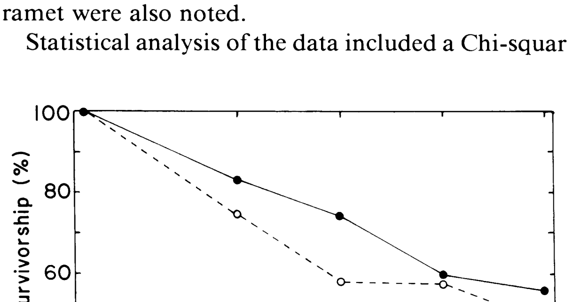

FIG. 3. Survivorship of severed ramets of *Lycopodium flabelliforme* located in relatively sunlit (○) and shaded (●) microsites.

test for distribution goodness of fit, analysis of variance, and least significant difference contrast comparison of means to determine significant differences at an alpha level of .05 (Zar 1984).

RESULTS

Interramet and interroot distance distributions in *L. flabelliforme* differed significantly ($\chi^2 = 136.37$, Fig. 1). While 68% of the ramets of a clone were 2–5 cm apart, 57% of the roots were >7 cm apart, with the mean interramet and interroot distances being 4.9 ± 0.3 cm and 8.3 ± 0.5 cm, respectively (Fig. 1). Over 40% of the roots on a genet were located <2 cm from a ramet and >25% of the roots were located >7 cm away from the nearest ramet; therefore, each ramet on a genet did not necessarily have a nearby root (Fig. 1). In addition, the average root-to-nearest-ramet distance was 5.1 ± 0.6 cm (Fig. 1).

An initial, relatively sharp decrease in the survivorship of severed ramets at the field site was followed by a small, but steady, trend for decreasing survivorship (Fig. 2). One month following severing, ramet survivorship had fallen to 49 ± 4% with the final observation on 25 October showing 41 ± 5% surviving. In contrast, throughout the observation period, the survivorship of intact ramets remained significantly greater than that of severed ramets. Intact ramets experienced 100% survivorship until August, thereafter showing a gradual decrease to 96 ± 1% by the final observation (Fig. 2). The survivorship of severed ramets located in relatively open microsites (PAR > 6.0 mol·m^{-2}·d^{-1}) was lower than that in shaded (<4.0 mol·m^{-2}·d^{-1}) microsites (Fig. 3). Five weeks after severing, survivorship of ramets was 58% in the open and 77% in the shaded patches, with continued higher survivorship in the shaded ramets through the final observations (Fig. 3).

Maximum xylem pressure potentials of *L. flabelliforme* in the field corresponded to precipitation patterns (Fig. 4). During the relatively dry months of June and July, the maximum xylem pressure potentials of intact ramets averaged ≈0.2 MPa greater than those of severed ramets. Similarly, minimum xylem pressure potentials reflected precipitation patterns and prevailing weather conditions, with significantly lower values occurring on relatively warm or low-humidity days (e.g., 14 July and 11 October) and higher values occurring on cool or rainy days (e.g., 19 August and 25 October). In general, minimum and maximum xylem pressure potentials of severed and intact ramets did not differ significantly, and when they did, there was no consistent pattern.

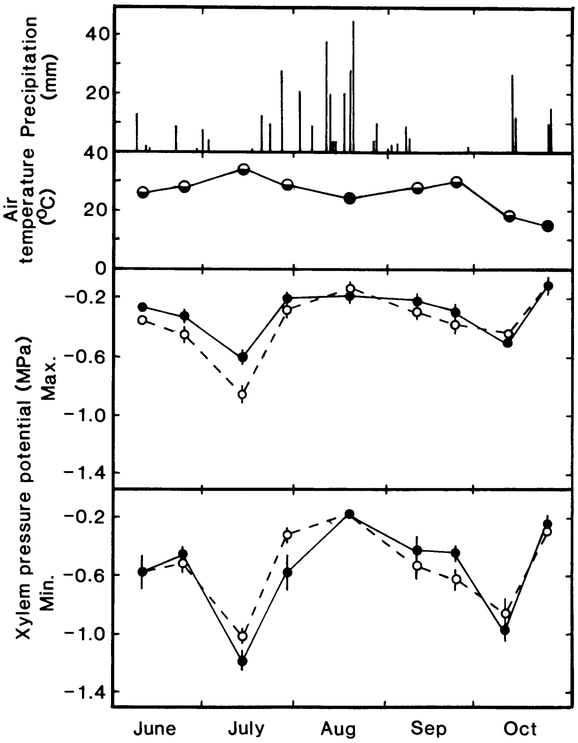

FIG. 4. Seasonal variation in precipitation, maximum air temperature on measurement days, and maximum and minimum xylem pressure potential for severed (○) and intact (●) ramets of *Lycopodium flabelliforme*. For air temperature, closed symbols indicate cloudy days and partially filled symbols indicate partly cloudy days. Vertical bars denote ±1 SE for the means of the xylem pressure potential measurements.

The capacitance, or total water storage within a particular region of a clone (cubic metres per megapascal), showed an order of magnitude greater storage in the crowns and in the roots than in the upright stems and the underground rhizome (Table 1). The capacitance

TABLE 1. Measurements of capacitance (total water storage within the given region of the clone) for four structural regions of *Lycopodium flabelliforme* clones. Values are means ± 1 standard error, and each mean is significantly different from each of the others ($\alpha = .05$).

Water storage			Crown	Upright stem	Underground rhizome	Root
Capacitance	(m^3/MPa)	$\bar{X}$	0.310 × 10^{-6}	0.059 × 10^{-6}	0.022 × 10^{-6}	0.423 × 10^{-6}
		±1 SE	±0.018 × 10^{-6}	±0.003 × 10^{-6}	±0.002 × 10^{-6}	±0.005 × 10^{-6}
Capacitance per unit water volume	(MPa^{-1})	$\bar{X}$	0.204	0.191	0.132	0.262
		±1 SE	±0.012	±0.010	±0.009	±0.003
Capacitance per unit tissue mass	(m^3·MPa^{-1}·g^{-1})	$\bar{X}$	0.904 × 10^{-6}	0.713 × 10^{-6}	0.477 × 10^{-6}	1.917 × 10^{-6}
		±1 SE	±0.053 × 10^{-6}	±0.037 × 10^{-6}	±0.032 × 10^{-6}	±0.022 × 10^{-6}

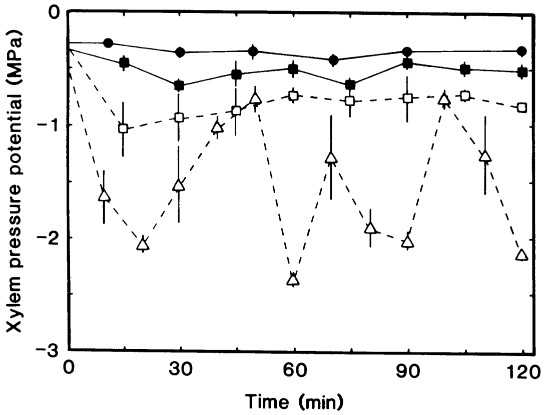

FIG. 5. Greenhouse measurements showing variations in *Lycopodium flabelliforme* xylem pressure potential for connected ramets of a genet kept in the dark at high humidity (●); an intact genet with half of the ramets illuminated (□) and half of the rametes kept in the dark at high humidity (■); and illuminated, severed ramet pairs (△). Vertical bars denote ±1 SE for the means.

per unit volume of water, or the reciprocal of the slope of the pressure-volume relationship (MPa^{-1}), was significantly higher (i.e., greater water storage) in the ramet crowns and in the roots than in the upright stems of the ramets and in the underground rhizome (Table 1). Similar results were found for capacitance per unit tissue mass (cubic metres per megapascal per gram).

In the physiological integration study, greenhouse measurements showed that the illuminated severed and intact genets had significantly lower water potentials than the control genet, which experienced xylem pressure potentials no lower than −0.4 ± 0.1 MPa (Fig. 5). Illuminated severed ramets reached significantly lower xylem pressure potentials (−2.3 ± 0.5 MPa) than did illuminated intact ramets, whose minimum value did not exceed −1.0 ± 0.3 MPa. The minimum xylem pressure potential of the shaded ramets connected to illuminated ramets was −0.7 ± 0.2 MPa. Thus, the dark intact ramets had xylem pressure potentials significantly lower than the controls but higher than the illuminated ramets to which they were connected, indicating that shaded ramets must translocate water to illuminated ramets (Fig. 5). The movement of xylem water along the rhizome was bidirectional because a comparison of the xylem pressure potentials of illuminated ramets basipetal and acropetal to the shaded ramets showed no statistical difference. The distance between shaded and illuminated ramets also appeared to have no significant effect on changes in the xylem pressure potentials of the former.

DISCUSSION

In the examination of water translocation among the ramets of *Lycopodium flabelliforme* in the heterogeneous light environment of the forest understory, measurements of root distribution contributed to the interpretation of the survivorship and physiological integration studies. With >50% of the roots on a clone >7 cm apart and ramets typically 2–5 cm apart, each ramet did not necessarily have an associated root. Thus, severed ramets in the survivorship study that lacked associated roots may have contributed to the disparity in severed vs. intact ramet survivorship. The distribution of roots along the rhizome suggested that some of the severed ramets were without roots and would be incapable of maintaining their own water status. Further, capacitance data indicated that water storage was greatest in ramet crowns and in roots; therefore, the ramets of a clone without associated roots must rely on water translocated from other ramets or from roots located near other ramets.

Although the survivorship studies (Fig. 3) displayed marked differences between severed and intact ramets, the xylem pressure potential patterns in the field were not as distinct. Higher xylem pressure potentials had been hypothesized for connected ramets, but this occurred only for the maximum xylem pressure potential measurements between May and August. The unexpected outcome may have resulted from the predominant survival of rooted, severed ramets in shaded microsites as opposed to those in more open, sunlit areas. Consequently, the severed ramets available for sampling were mainly shaded, while intact ramets available for sampling were not thus limited. This conclusion is supported by the ramet survivorship study of sunlit and shaded clones wherein severed ramets from shaded clones had greater survivorship. However, the fluctuating xylem pressure potential pattern for severed ramets in the greenhouse experiment indicated that stomatal closure may occur when the ramets are stressed. Thus, the similarity in the xylem pressure potentials between severed and intact ramets in the field may also have been due to stomatal closure in the severed ramets in response to water stress, causing a subsequent increase in xylem pressure potential.

Measurements of genet water storage provided further insight in the understanding of ramet water status. Previous clonal integration studies have stressed the importance of the rhizome as a storage organ, especially for carbohydrates (Ashmun et al. 1982, Flanagan and Moser 1985). Water storage in *L. flabelliforme* clones, regardless of the units used to describe capacitance, was highest in the roots and the ramet crowns. In this species, the rhizome appears to be more important for water transport between ramets, because rhizome capacitance was low and the survivorship of ramets with severed rhizomes was considerably lower than for those with intact rhizomes. The low water storage capacity of the rhizome reinforces the importance of root distribution relative to ramet distribution in maintaining ramet water potential for *L. flabelliforme*.

The greenhouse physiological integration study verified the ability of the rhizome to translocate water.

Severed ramet xylem pressure potentials were significantly lower when compared with the intact treatments. Illumination for 15 min caused a decrease of 0.7 MPa in the xylem pressure potentials of intact ramets connected to shaded ramets. Thirty minutes following illumination of sibling ramets, the shaded, connected ramets also experienced decreased xylem pressure potentials, regardless of whether they were basipetal or acropetal to the illuminated ramet and regardless of the distance between shaded and illuminated ramets. This evidence suggesting bidirectional water transport between ramets is similar to the findings of Salzman and Parker (1985), which related clonal integration in the rhizomatous species *Ambrosia psilostachya* to heterogeneity in the salt environment in the soil. Reversed flow in the xylem caused by water deprivation have been demonstrated for the stoloniferous species *Saxifraga sarmentosa* (Quereshi and Spanner 1971). Alpert and Mooney (1986) also demonstrated bidirectional water movement in the rhizomatous herb *Fragaria chiloensis.*

Within deciduous forests, irradiance varies in space and time (Hutchinson and Matt 1977). Based on the greenhouse physiological integration study, this heterogeneity in the light environment is significant enough to result in water translocation between ramets of *L. flabelliforme* acting in response to the related changes in ramet xylem pressure potentials. This xylem integration pattern suggests adaptive advantages similar to those proposed for several other clonal species. Specifically, resource sharing among ramets may buffer the effects of unfavorable microsites in environments consisting of a mosaic of favorable and unfavorable sites (Alpert and Mooney 1986, Pitelka and Ashmun 1986). In environments where heterogeneous distributions of different resources yield a mosaic consisting only of unfavorable microsites, resource sharing may allow for the survival of established clones (Alpert and Mooney 1986). These proposed benefits of clonal integration identify the need for coinciding examinations of the distributions of each of the resources affecting a clone. The accurate assessment of the adaptive advantages of clonal integration may involve the consideration of resource interactions that could alter the influence of each particular resource on integration patterns.

ACKNOWLEDGMENTS

The Department of Biology at Virginia Commonwealth University provided funding for a portion of this study. Mr. J. Lewis Payne and Ms. Betty J. Lau provided field assistance.

LITERATURE CITED

Alpert, P., and H. A. Mooney. 1986. Resource sharing among ramets in the clonal herb, *Fragaria chiloensis.* Oecologia (Berlin) **70**:227–233.

Ashmun, J. W., R. J. Thomas, and L. F. Pitelka. 1982. Translocation of photoassimilates between sister ramets in two rhizomatous forest herbs. Annals of Botany **49**:403–415.

Flanagan, L. B., and W. Moser. 1985. Patterns of ^{14}C assimilate distribution in a clonal herb, *Aralia nudicaulis.* Canadian Journal of Botany **63**:2111–2114.

Ginzo, H. D., and P. H. Lovell. 1973. Aspects of the comparative physiology of *Ranunculus bulbosus* L. and *Ranunculus repens* L. I. Response to nitrogen. Annals of Botany **37**:753–764.

Hartnett, D. C., and F. A. Bazzaz. 1983. Physiological integration among intraclonal ramets in *Solidago canadensis.* Ecology **64**:779–788.

Harvill, A. M., Jr., C. E. Stevens, and D. M. E. Ware. 1979. Atlas of the Virginia flora. Part 1. Virginia Botanical Associates, Farmville, Virginia, USA.

Hutchinson, B. A., and D. R. Matt. 1977. The distribution of solar radiation within a deciduous forest. Ecological Monographs **47**:185–207.

Marshall, C., and G. R. Sagar. 1968. The distribution of assimilates in *Lolium multiflorum* Lam. following differential defoliation. Annals of Botany **32**:715–719.

Nobel, P. S., and P. W. Jordan. 1983. Transpiration stream of desert species: resistances and capacitances for a C_3, a C_4, and a CAM plant. Journal of Experimental Botany **34**: 1379–1391.

Pitelka, L. F., and J. W. Ashmun. 1986. Physiology and integration of ramets in clonal plants. Pages 399–435 *in* J. B. C. Jackson, L. W. Buss, and R. E. Cook, editors. Population biology and evolution of clonal organisms. Yale University Press, New Haven, Connecticut, USA.

Pitelka, L. F., D. S. Stanton, and M. O. Peckenham. 1980. Effects of light and density on resource allocation in a forest herb, *Aster acuminatus* (Compositae). American Journal of Botany **67**:942–948.

Quereshi, R. A., and D. C. Spanner. 1971. Undirectional movement of tracers along the stolon of *Saxifraga sarmentosa.* Planta **101**:133–146.

Raphael, D. O., and P. S. Nobel. 1986. Growth and survivorship of ramets and seedlings of *Agave deserti*: influence of parent-ramet connections. Botanical Gazette **147**:78–83.

Ryle, G. J. A., and C. E. Powell. 1972. The export and distribution of ^{14}C-labelled assimilates from each leaf on the shoot of *Lolium temulentum* during reproductive and vegetative growth. Annals of Botany **36**:363–375.

Salzman, A. G., and M. A. Parker. 1985. Neighbors ameliorate local salinity stress for a rhizomatous plant in a heterogeneous environment. Oecologia (Berlin) **65**:273–277.

Schellner, R. A., S. J. Newell, and O. T. Solbrig. 1982. Studies on the population biology of the genus *Viola.* IV. Spatial patterns of ramets and seedlings in three stoloniferous species. Journal of Ecology **70**:273–290.

Tietema, T., and F. van der Aa. 1981. Ecophysiology of the sand sedge, *Carex arenaria* L. III. Xylem translocation and the occurrence of patches of vigorous growth within the continuum of a rhizomatous plant system. Acta Botanica Neerlandica **30**:183–189.

Zar, J. H. 1984. Biostatistical analysis. Prentice-Hall, Englewood Cliffs, New Jersey, USA.