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RECOVERY OF BAZZANIA TRILOBATA (L.) S.GRAY FOLLOWING DESSICATION

RECOVERY OF

BAZZANIA TRILOBATA (L.) S. Gray

FOLLOWING DESSICATION

by

Mary C. Sollows

A THESIS PREPARED IN PARTIAL FULFILLMENT OF

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Abstract

Bazzania trilobata (L.) S.F. Gray is a common leafy liverwort on the floor of closed canopy mixed and coniferous forests in New Brunswick. It may be a suitable indicator of biodiversity depending on its ability to adapt to forestry-related environmental stresses, however published information regarding this species is scant. This study uses a novel approach to assess the species' ability to tolerate various drying regimes. Tolerance, indicated by continued metabolic activity, was quantified by measuring respiration and photosynthetic rates, shoot growth and colour. Samples of *B. trilobata* collected from a closed forest were subjected to drying in either full sun or in shade conditions. Samples (field-dried) were collected from a clear-cut area adjacent to the forest. Baseline data were recorded for all samples as well as for fresh samples (controls). All samples were given a recovery period of high humidity, low light intensity, and moderate temperatures. Post recovery measurements were compared to the base-line data.

Metabolic activity and shoot length, of the field-dried samples increased and colour shifted from yellow toward green following the recovery period, suggesting that they are able to remain viable for at least two years following a clear-cut forest disturbance, and ultimately to recover. Metabolic activity and shoot length did not increase and colour shifted from green toward brown for sun-dried and shade-dried samples, suggesting the conditions associated with these treatments were beyond the dessication tolerance range of *B. trilobata*.

Given its easy visual identification and sensitivity to dessication, *B. trilobata* may be a useful indicator of a specific range of environmental conditions associated with closed forest communities. It may be useful in determining which forest-harvest technique causes the least change to these conditions, with the ultimate goal of maintaining native biodiversity.

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INTRODUCTION

The ability of organisms to survive and reproduce depends on their ability to tolerate environmental conditions, including stress. Stresses may be periodic, such as seasonal variations in temperature, or they may occur unpredictably, such as fire. Anthropogenic stresses, such as those associated with forestry practices, are commonly imposed upon many species in most regions of the world. Canopy removal, a major stress resulting from forestry practices, may cause damage due to decreased relative humidity, increased ambient temperatures, cell damage from high light intensity, or a combination of these factors. The degree of damage to a species varies according to the range of tolerance to altered environmental conditions.

The development of criteria for forest management activities is the focus of current studies in New Brunswick and elsewhere (Canadian Council of Forest Ministers 1995). The complexity of a forest ecosystem is such that it is necessary to measure selected components to derive information about ecosystem conditions. Identification of species that are good indicators (indicator species) of forest conditions is important in evaluating and predicting the effects of forest management activities (Woodley and Forbes 1997).

Biodiversity

The success of organisms following any disturbance depends on their ability to survive and reproduce using resources available in the altered environment (Boyle 1991). Species that are lost following a disturbance provide space and resources for species that are able to tolerate the conditions. There is a high diversity of ecosystem components following natural disturbances (native diversity) and recommended forest management practices should

maintain this native diversity (Woodley and Forbes 1997).

Biodiversity is a concept that refers to the variety of organisms in a particular area or region. There are three major categories of biodiversity: (1) genetic, (2) species, and (3) ecosystem biodiversity. Genetic diversity refers to the variety of genotypes within a species. Species diversity refers to the variety of species within a region. Two measures of species diversity are species richness and taxonomic diversity, including the evolutionary relationship of species to each other. Ecosystem diversity refers to the variety of composition, structure and function within a defined area. Composition includes the identity and variety of organisms, structure refers to the physical organization at a landscape level and function involves ecological and evolutionary processes including gene flow, disturbances and nutrient cycling within a community (Boyle 1991).

Conservation of the native biodiversity of an ecosystem is important in maintaining the complex interactions that sustain the ecosystem (Boyle 1991). Organisms play a major role in nutrient recycling, soil quality, watershed management, disease and pest control and pollination. Reduction in biodiversity at one level of organization may have detrimental effects on physical, chemical and biological systems at the same or different levels (Woodley and Forbes 1997). For example, the loss of a plant species can reduce the moisture or nutrient content of the soil making the soil unsuitable for other species. Bryophytes are important in succession of terrestrial systems and play an important role in nutrient recycling. They play an important role in the production of phytomass in various systems such as tundra communities. Bryophytes stabilize moisture and temperature levels of soil, prevent soil erosion and provide substrates for insects and animals (Longton 1984). These functions are all important components of terrestrial ecosystems which may also indirectly influence aquatic ecosystems.

Conservation of biodiversity in forests is a major concern to both proponents and opponents of the forest industry, however protection of forested land varies with geographical area, its designated land use, and its ownership. In New Brunswick, legislation requires a 30m band of forest (buffer strip) be left on both sides of a watercourse in harvested areas for protection of water quality. Buffer strips also protect natural habitats and provide movement corridors for wildlife (Woodley and Forbes 1997). Trees can be harvested to the edge of the buffer strip, resulting in an abrupt and dramatic change in the environmental conditions due mainly to the removal of the forest canopy.

The degree of contrast between the closed forest and a harvested area depends on the harvesting technique employed. Clear-cutting is a forest management tool that is used frequently in New Brunswick. It involves the felling of most trees within a specified area, although some mature trees of a "desirable" species may be left standing as a source of propagules. Studies on the effects of clear-cutting on biodiversity have provided mixed results. For example, diversity indices (which reflect the number of species present) are often high in a managed clear-cut. However, these species may not be the same as those present in the forest before the clear-cut. The post-harvest invasion of different (often pioneer) species represents an alteration of the ecosystem and may prevent the re-establishment of the pre-harvest species (Boyle 1991).

Indicators of biodiversity

Species used as biodiversity indicators should show sensitivity to changes in environmental conditions without risk of population failure. Directly monitoring population trends and the physiology and morphology of sensitive plants or animals can provide direct feedback on the status of that species and its habitat requirements processes, or indirect

feedback on species or processes that are closely linked to the indicator. A useful indicator should be practical to monitor and provide early warnings of conditions which suggest a deterioration of native biodiversity (McKenney et al. 1994).

As part of a long-term study at the Hayward Brook Watershed, Westmorland County, N.B., which is monitoring forest floor biodiversity following clear-cutting (Parker 1997), an indicator species is sought for the closed forest bryophyte community. *Bazzania trilobata* (L.) S.F. Gray may be a potential indicator species for biodiversity in the bryophyte community in mixed and coniferous forests in New Brunswick. Unlike many bryophytes, it is large and easily identified in the field. It also appears to respond quickly and visibly to canopy removal, as evidenced by dramatic changes in appearance following forest harvest.

The study organism

Bazzania trilobata is a leafy liverwort of the Subfamily Bazzaniodeae, Family Lepidoziaceae, Order Jungermanniales, Class Hepaticae (Smith 1990). It is common in temperate and warm temperate climates, in humid, low-light intensity areas, on moist rocks, soil, bases of trees and on rotting wood and is not found on calcareous substrates (Schuster 1969; Hicks 1992). The plants grow in close contact with the substrate which allows for water absorption and minimal evaporation (Hicks 1992). In very humid conditions as often occur under evergreens and conifers in the northern part of its range, it is green and shiny and can form large, deep tufts. *B. trilobata* is often found growing near *Sphagnum* spp. (Schuster 1969).

All parts of the gametophyte are photosynthetic, containing chlorophylls *a* and *b* which are responsible for the green colour of the plants. The large amount of chlorophyll/ protein complex is comparable to lignified (vascular) shade plants (Schofield 1985).

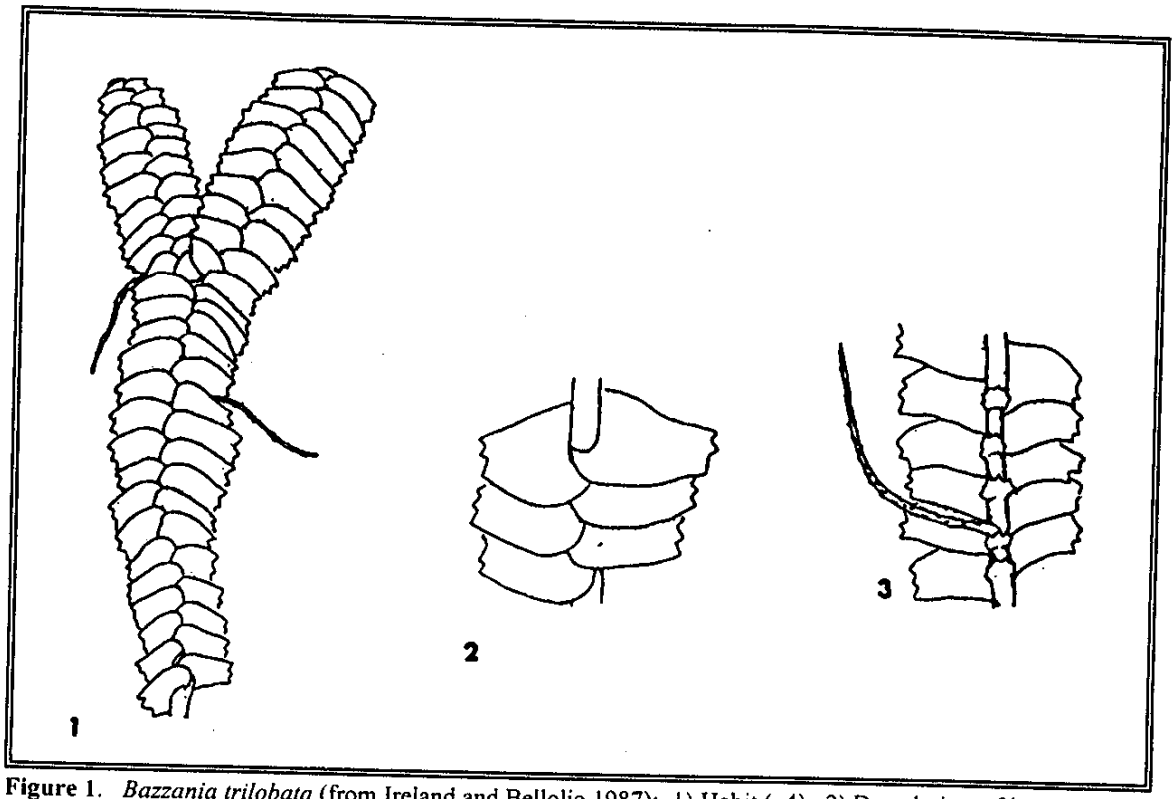

Figure 1. *Bazzania trilobata* (from Ireland and Bellolio 1987): 1) Habit (x4), 2) Dorsal view of leaves (x9), and 3) Ventral view of leaves (x9).

This species is recognized by its two rows of overlapping convex leaves (phyllidia) on the dorsal surface (Figure 1). A row of smaller leaves is found on the ventral side along the midrib. The morphology and habit of *B. trilobata* vary with environmental conditions (Ireland and Bellolio 1987). In humid, shaded areas it grows as deep green tufts 10 to 15 cm in height. In drier conditions, it is reduced in size (Schuster 1969). It has also been described as whitish in colour when dry (Smith 1990).

The leaves of most liverworts are only one cell layer thick with neither a vascular system nor cuticle (waxy, extra-cellular protective surface layer). External water conduction is very important in liverworts. The shape and arrangement of leaves is thought to influence the system of external capillary movement of water (Basile and Basile 1987). The absence of a cuticle allows the plant to absorb water and dissolved nutrients over its entire surface,

however it also means the plant cannot prevent the loss of water from its cells in a dry environment (Gaber and Hutchinson 1988).

This simple anatomy also means that nutrient uptake by the liverworts is strongly influenced by the plants which form the canopy. As water falls from the leaves (throughfall) and down stems (stemflow) of the canopy, nutrients are transferred to the forest floor. These nutrients are both leached from the vegetation and washed from the surface of the vegetation. Removal of the canopy therefore influences nutrient availability to the organisms below (Eaton *et al.* 1973; Cronan and Reiners 1983).

Tolerance of dessication for most bryophytes is greater if dessication occurs slowly (Chopra and Kumra 1988). Changes in leaf position, including curling of the edges during drying, may slow dessication. Some bryophytes also show seasonal variations in dessication tolerance (Bewley and Thorpe 1974; Dilks and Proctor 1976). Many bryophytes have a physiological drought resistance; they may appear dry and brittle under drought conditions but they may still be alive (Hicks 1992). Many bryophytes undergo cell damage and a change in metabolic activity upon dessication. This may be due to damaged chloroplast pigments and/or ruptured cell membranes (Brown and Bates 1990). Ruptured membranes are a common occurrence in drought sensitive mosses and liverworts during drying. This causes cell contents to leak, increasing dessication and the permeability of the cell membrane. This in turn affects nutrient transfer (Brown and Bates 1990). Some bryophytes can survive dessication for a number of years, however other species may be irreversibly damaged by prolonged dessication (Gerdol *et al.* 1996).

Sexual reproduction is accomplished by spores produced between June and August (Schuster 1969). For most liverworts, development of gametangia (sexual organs) requires an increase in light and temperature (Chopra and Kumra 1988).

Unlike mosses, liverwort spores are released within a short period. Vegetative propagation from unspecialized tissue is common in *B. trilobata* (Schuster 1969). Regeneration of tissues or organs which have been damaged or removed is influenced by light, humidity, temperature, pH, season and degree of wounding (Chopra and Kumra 1988).

Current research projects involving *B. trilobata* relate to the presence of sesquiterpenoids (Konig *et al.* 1996; Nagashima *et al.* 1996). These compounds, which are thought to deter herbivory, are unique to particular species and may be useful for taxonomic purposes. The terpenoids are found within the numerous complex oil bodies of leaf cells of *B. trilobata* (Schofield 1985).

CO_2 metabolism

Bryophytes are photoautotrophic, i.e. they capture energy and carbon through photosynthesis which can be summarized by the general equation:

$$6CO_2 + 12H_20 + \text{Light} \rightarrow C_6H_{12}O_6 + 6O_2 + 6H_2O$$

During photosynthesis the plant removes carbon dioxide from the air and uses light energy, captured by pigments, to split water molecules. The energy trapped during photosynthesis is used via aerobic respiration, in which chemical energy stored in the bonds of carbohydrates is transferred to ATP (adenosine triphosphate, an energy-carrier molecule) when needed (Hall and Rao 1972). The health of a bryophyte can be measured by quantifying its metabolic activity. Since respiration is used for (1) maintenance and repair and (2) growth, a shift in balance between respiration and photosynthesis should change if (i) membranes and/or chloroplasts pigments are damaged and/or (ii) growth is occurring. At a constant light intensity and quality, a reduction in net photosynthesis indicates damage (Gerdol *et al.* 1996), e.g. of the pigment molecules or the membrane in which they are

embedded.

The infrared gas analyzer (IRGA) can be used to measure the changes in CO_2 concentration surrounding a plant sample in a glass cylinder. The chamber that holds the plant sample is made to fit the sample and can be very simple if IRGA measurements are conducted at room temperature (Bourdeau and Woodwell 1965). Based on the principle that CO_2 absorbs specific wavelengths of energy, infrared radiation is emitted from two filaments and passes down tubes through which sample gases are pumped. One tube carries the gas of unknown composition (i.e. from the area surrounding the plant) and the other carries a gas of known composition (Legg and Parkinson 1968).

Some of the radiation is removed by the CO_2 in the tubes while the remainder passes to a detector unit. The detector unit is filled with pure CO_2 and is sensitive only to the infrared wavelengths absorbed by the CO_2 (Legg and Parkinson 1968). It measures the difference in infrared absorption between the two tubes, from which the absorbed concentration can be calculated. During photosynthesis, the machine will detect a decrease in the concentration of CO_2 after the known gas mixture passes over the plant sample (Parkinson and Legg 1971).

Respiration does not require light, hence it occurs alone or simultaneously with photosynthesis. Because respiration releases CO_2, and photosynthesis absorbs CO_2 it is possible to detect metabolic activity by measuring the amount of CO_2 removed or added to the atmosphere (Raven *et al.* 1992). Since respiration occurs at the same time as photosynthesis, a measurement in the light will give only a net value. Analysis of the same sample in the dark will indicate the CO_2 change due to respiration. This value can be added to the value obtained during the light reaction to indicate the change due to photosynthesis alone (Brewer 1994). Thus the gross gain in carbon due to photosynthesis minus the loss of

carbon due to respiration is equal to the net gain in carbon due to photosynthesis.

Respiration rates (which are determined in the dark) indicate the use of photosynthetic products for maintenance and repair and/or growth and reproduction. Net photosynthetic rates indicate how the plant is allocating its surplus energy and resources. A positive net photosynthetic rate (photosynthesis exceeds respiration) suggests that the plant is able to store or utilize its resources for growth and reproduction. If there is no positive net photosynthetic rate (respiration exceeds photosynthesis), the plant may still be metabolically active as it repairs or maintains itself but there are not enough resources for growth and reproduction.

Objective and rationale

Preliminary observations of populations of *Bazzania trilobata* showed marked variation in colour, texture and abundance between harvested and closed canopy forests. Colonies in clear-cut stands appeared to be pale, yellow to whitish (Figure 2) and brittle compared to those in unharvested stands (Figure 3). Dense tufts were noted in both areas but were more numerous in the forest area. The differences were postulated to be related to the high light intensity and low relative humidity associated with canopy removal. Neither the tolerance of *Bazzania trilobata* to periods of dessication, nor its ability to regenerate following dessication are known. (For this study, tolerance is defined as the resumption or increase in metabolic activity following a period during which stressed samples were allowed to recover under favourable environmental conditions.)

The objective of this study is to determine the environmental tolerance of the leafy liverwort *Bazzania trilobata* to a range of drying treatments. The hypothesis is that *B. trilobata* will show a different tolerance to drying treatments which will be detectable in

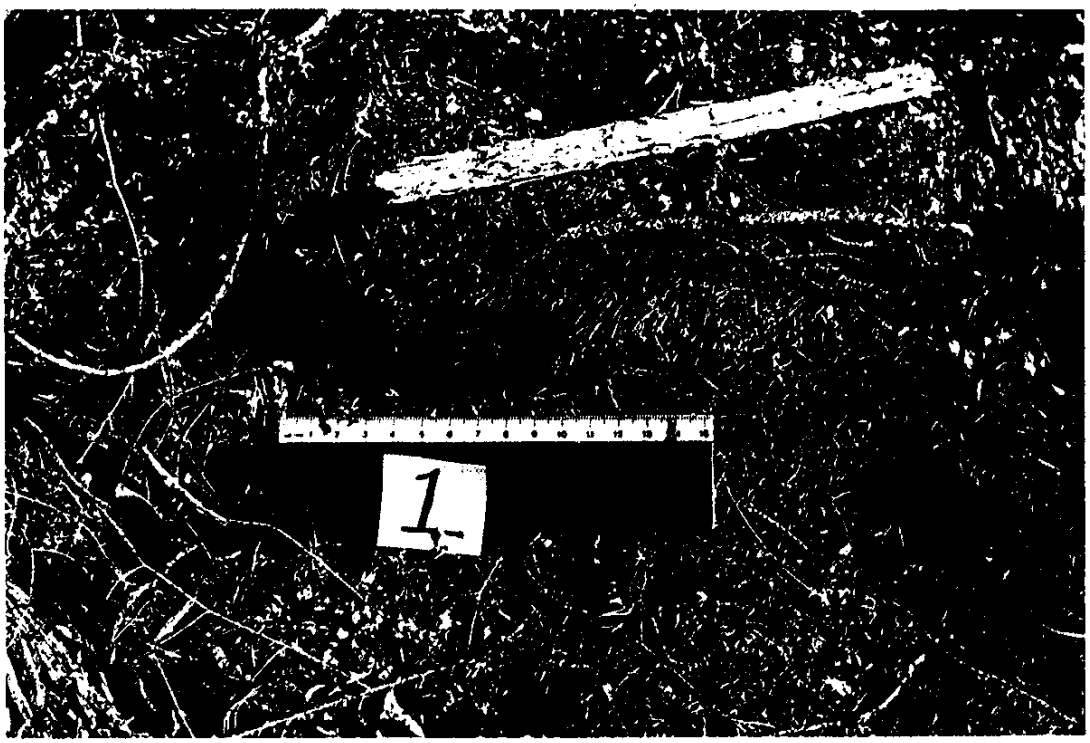

Figure 2. *Bazzania trilobata* colonies (above scale) in a clear-cut harvest area at the Hayward Brook study site, Fundy Model Forest, N.B. Numeric labels in the photograph are for slide identification only.

terms of its ability to recover. Differences in recovery may be manifested in (1) pigment recovery, i.e. a colour change from yellow to green, (2) a resumption of metabolism, i.e. increase in the CO_2 uptake during photosynthesis or increase in CO_2 production during respiration, as measured by infra-red gas analysis, or (3) shoot growth, i.e. elongation.

Figure 3. *Bazzania trilobata* colonies (above and to left of scale) in a closed canopy forest area at the Hayward Brook study site, Fundy Model Forest, N.B. Numeric labels in the photograph are for slide identification only.

MATERIAL AND METHODS

Study site

Bazzania trilobata was collected from Hayward Brook, Westmorland County, New Brunswick (45.88°N, 65.18°W) which is a site of on-going studies of forest-floor biodiversity (Figure 4). Samples were collected from two areas: (a) a buffer strip extending 60m on either side of the brook representing the closed canopy mixed forest, and (b) the adjacent harvested (clear-cut) stands. The canopy of the buffer strip was dominated by spruce (*Picea* species) and fir (*Abies balsamea* (L.) Mill.). The harvested area had been clear-cut in 1995 and was characterized by stumps and areas of slash. It had an open canopy with sparsely distributed young deciduous trees (e.g. *Populus tremuloides* Michx.) and saplings of *Picea* spp.

Sequence of procedures

Experimental procedures were conducted in the following sequence: (1) sample collection, (2) experimental manipulation consisting of drying treatments, (3) assessment of parameters (CO_2 utilization and colour and shoot length), (4) recovery period, (5) reassessment of parameters (CO_2 utilization, colour analysis and shoot length) and (6) statistical comparison of parameters before and after recovery.

Collection and experimental manipulation

Collections of *B. trilobata* were made on July 28, 1997 from the buffer strip and October 25, 1997 from both the buffer strip and the clear-cut. Four regimes were tested, corresponding to a range of temperature/light conditions (Table 1). (1) Control samples (collected from the buffer strip October 25, 1997) were analyzed within 5 days following collection. These represented healthy samples not subjected to drying treatments. (2) Field

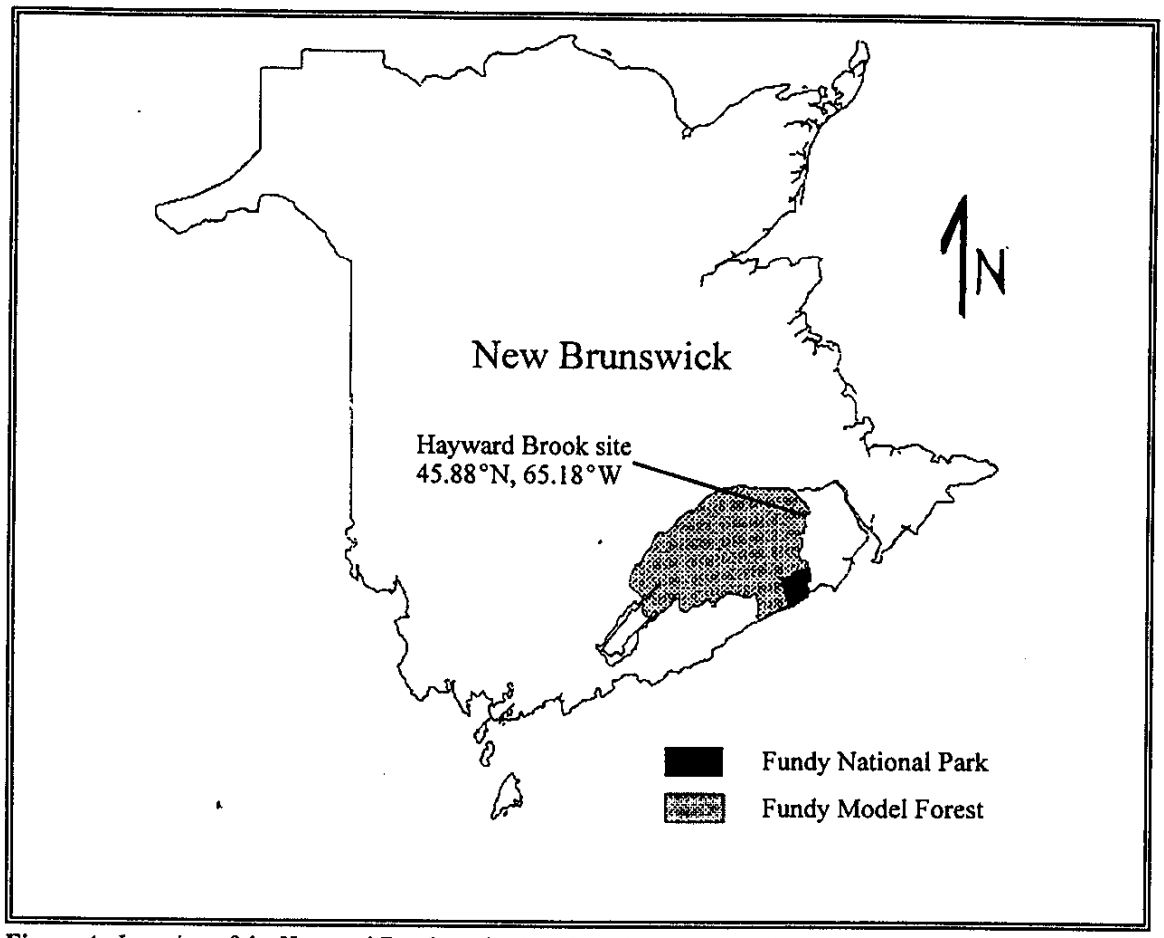

Figure 4. Location of the Hayward Brook study site where *Bazzania trilobata* was collected for experimental analysis of its recovery ability following dessication. Approximate scale 2 300 000 : 1.

samples (collected from the clear-cut October 25, 1997) had been subjected to an unknown but natural drying regime during the 2 years prior to this study. In the clear-cut, samples were presumed to have been subjected to higher light intensity, higher temperature and lower relative humidity than those in the adjacent buffer strip. Field-dried samples were analyzed within 9 days following collection.

Samples for two drying treatments were collected from the buffer strip July 28, 1997, taken to Quispamsis, Kings County, New Brunswick and divided into groups. Clumps of *B. trilobata* were separated into individual shoots to facilitate drying. They were randomly assigned to one of two different drying treatments. (3) Shade-dried samples were placed out

Table 1. Experimental treatments applied to *Bazzania trilobata* samples collected from Hayward Brook, N.B. Each treatment used 80 replicate groups of 10 shoots each (n = 800).

Treatment	Collection	Drying Regime			Location of drying treatment
		Temperature	Light	Storage	
(1) Control	Oct. 25/97 Buffer strip Hayward Brook	N/A	N/A	Cool, moist, Diffused light 1 - 5 days	N/A
(2) Field-dried	Oct. 25/97 Clear-cut areas adjacent to buffer strip Hayward Brook	Assumed to be higher temperature than controls approx. 2 years	High light intensity	Cool, moist, Diffused light 5 - 9 days	Field (Hayward Brook clear-cut area)
(3) Shade-dried	July 28/97 Buffer strip Hayward Brook	Mean mid-day temp.:24.6°C 28 days	Diffused light	Diffused light Mean mid-day temp.: 20.4°C 60 days	Lab
(4) Sun-dried	July 28/97 Buffer strip Hayward Brook	Mean mid-day temp.: 32°C 28 days	Full sun	Diffused light Mean mid-day temp.: 20.4°C 60 days	Lab

of direct sunlight. (4) Sun-dried samples were placed in a greenhouse. For both regimes, fans were used at low speed to increase air circulation. Temperatures were recorded every 8 seconds using ACR Systems Inc. XT-100 temperature sensors. After 28 days of drying from July 30 - August 28, 1997, samples were stored in a cool dark room until analyses (description follows) began November 1, 1997.

Assessment

Immediately following drying treatments, samples of each treatment and the controls were subdivided into two groups. Half (400 shoots each treatment + control) was analyzed

destructively for CO_2 utilization (using IRGA). The remaining half (400 shoots from each treatment + control) was assessed for colour and shoot length, then given the period of recovery, during which the shoots were subjected to favorable conditions of low light and high humidity described above. At the end of the 2 month recovery period, colour, shoot length and CO_2 utilization were re-assessed on all samples.

CO_2 utilization. Forty replicates of 10 shoots each were analyzed for CO_2 utilization using a series 225 Gas Analyzer (IRGA) from the Analytical Development Company, Ltd (Hoddeson, England). All shoots were rehydrated with distilled water for approximately one hour prior to analysis. Excess water was removed by patting samples with paper towels. These steps removed non *B. trilobata* matter and hydrated the samples to a point at which metabolism resumed (and CO_2 readings could be taken).

Samples were placed in a glass cylinder over which a reference gas (medical air: certified 350 ppm CO_2) was passed. The difference between the amount of carbon dioxide in the reference air versus the air recovered after passing over the sample was determined. Readings were taken at plateaux of photosynthesis and respiration as recorded on a Fisher Recordall Series 5000 chart recorder. Samples were first run in the dark (to measure respiration alone) by covering the cylinder with aluminum foil. The foil was then removed and the analysis was repeated in the light. Light for photosynthesis was supplied by Sylvannia GroLux wide spectrum F40GRO-WS 40W bulbs. Light intensity was measured by a light meter Model Li-185A and a quantum sensor Model Li-190S from Li-cor Limited (Lincoln, Nebraska).

After IRGA processing, samples were oven-dried at 100°C for approximately 10 hours to obtain the dry-weight. Respiration, net photosynthetic and gross photosynthetic rates were expressed in mg carbon·g dry weight^{-1}·hr^{-1} for each sample.

Shoot length, colour analysis and recovery. The length of individual shoots was measured before the recovery period and the difference in shoot lengths was calculated to determine the change in shoot length (regrowth) during the recovery period. Before and after the recovery period, the colour of the terminal 1 cm of each shoot was analyzed for colour using Munsell Colour Charts for Plant Tissue (Wilde and Voigt 1977) (Figure 5).

Recovery period

After storage, individual shoots were cut to a standard length of 2 cm. Branches, rhizoids and apical tips were removed to standardize shoots. Forty replicates of 10 shoots each were planted horizontally in plastic growth trays on a substrate of crumbled decaying organic matter (1cm thick) overlaying 6 cm of inert vermiculite. The organic substrate was collected in the buffer strip at the Hayward Brook site under green, healthy-looking *B. trilobata* colonies.

Samples were placed under Sylvannia GroLux wide spectrum F40GRO-WS 40W bulbs for 2 months at the Quispamsis site. Light was supplied for a period of 12 hr light : 12 hr dark and 20 - 30 $\mu\varepsilon/m^2 \cdot s$ (an intensity comparable to shaded forest conditions). Shading was accomplished by placing two layers of screening fabric placed above the samples. Temperature and light intensities were measured daily and samples were misted on alternate days using rain water collected in September from the Hayward Brook buffer strip.

Statistical analyses

Respiration, net photosynthesis and gross photosynthesis of each treatment were compared before and after the recovery period. Statistical significance of differences was evaluated by a two-way ANOVA (SAS Institute Inc., 1989) with (a) drying treatment and (b)

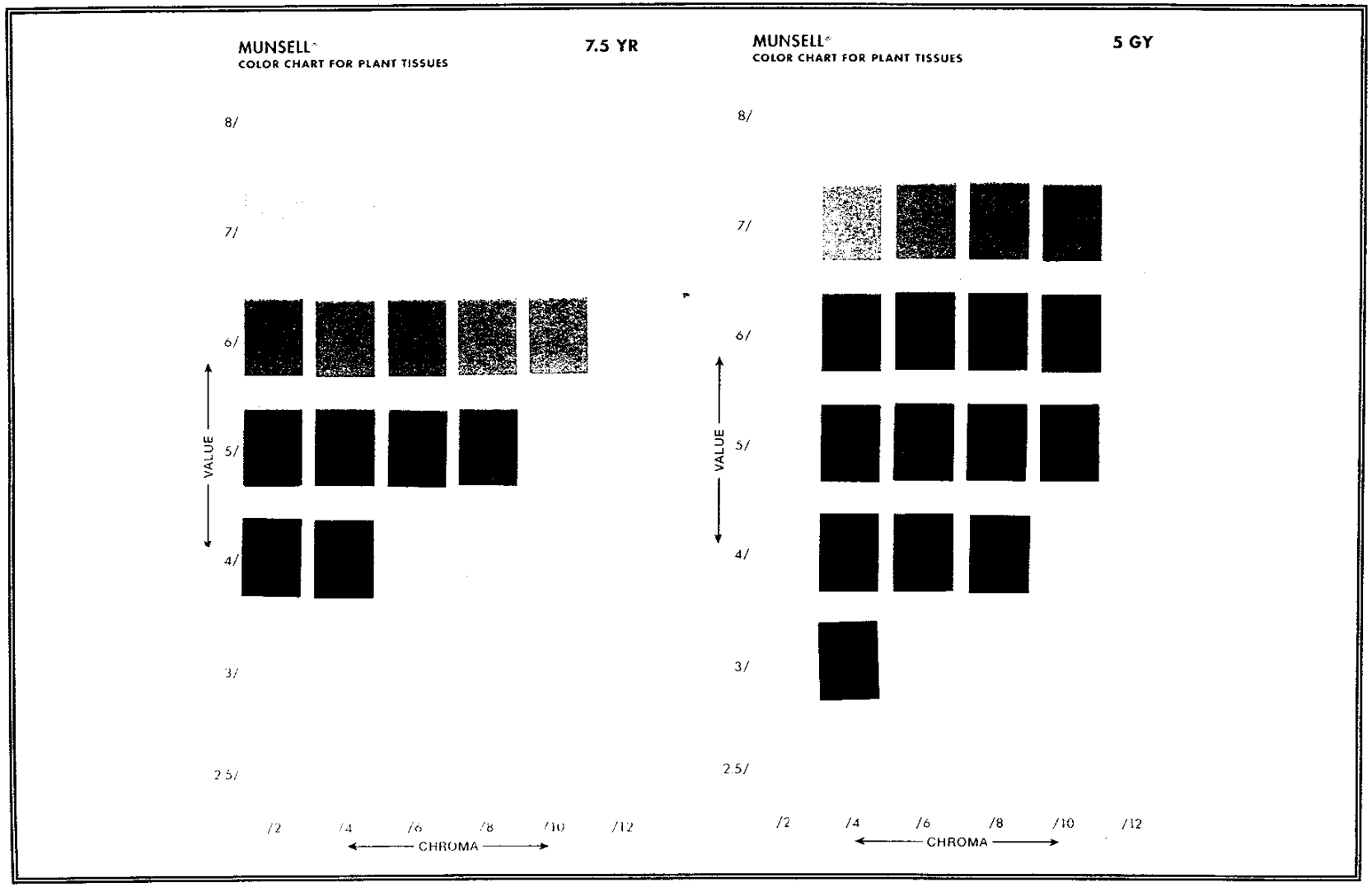

Figure 5. Reproduction of the 2 Munsell* colour charts that bound the range of colours (7.5YR to 5GY) exhibited by 1599 of 1600 *Bazzania trilobata* specimen shoots (Taken from Wilde and Voigt, 1977). Colours may be altered as a result of reproduction.

before *vs.* after recovery as main effects. The change in shoot length during the recovery period was compared among treatments using a one-way ANOVA. Tukey's Studentized Range (HSD) Test was applied to interactions and main effects showing significant differences. All differences were tested at $p < 0.05$ unless otherwise noted. Colour was assessed visually, using frequency distributions.

RESULTS

General observations

The samples collected from the buffer strip were considered to be healthy specimens: the dense green mats of pliant, moist shoots were robust in appearance. In contrast, colonies in the clear-cut were neither as large nor as dense as in the buffer strip. These mats found in the clear-cut areas were brittle and yellow in colour when viewed from above. Small areas of green shoots were observed at the centre of and in some areas under the mat. Some shoots which appeared yellow from above, retained green portions closer to the base of the colony.

Infra red gas analyses

Respiration. All samples showed evidence of respiration activity before and after the recovery period, indicating viability. Analysis of variance indicated that respiration rate differed significantly among treatments ($F=237.29$, $P=0.0001$) and before and after recovery ($F=15.38$, $P=0.0001$) (Appendix I). There was a significant interaction between treatment and recovery effects ($F=29.20$, $P=0.0001$).

Overall, the field-dried samples exhibited the highest mean respiration (Figure 6). Respiration rates for shade and sun-dried samples were equal and were the lowest of the treatments; mean respiration for the control samples was intermediate. The pooled treatments showed higher mean respiration following recovery than before.

In terms of interactions, there were no significant differences in mean respiration rates before and after recovery for the field-dried and shade-dried treatments (Figure 6). However both control and sun-dried treatments showed higher respiration rates following the recovery period.

Gross photosynthesis. All samples showed evidence of gross photosynthetic activity

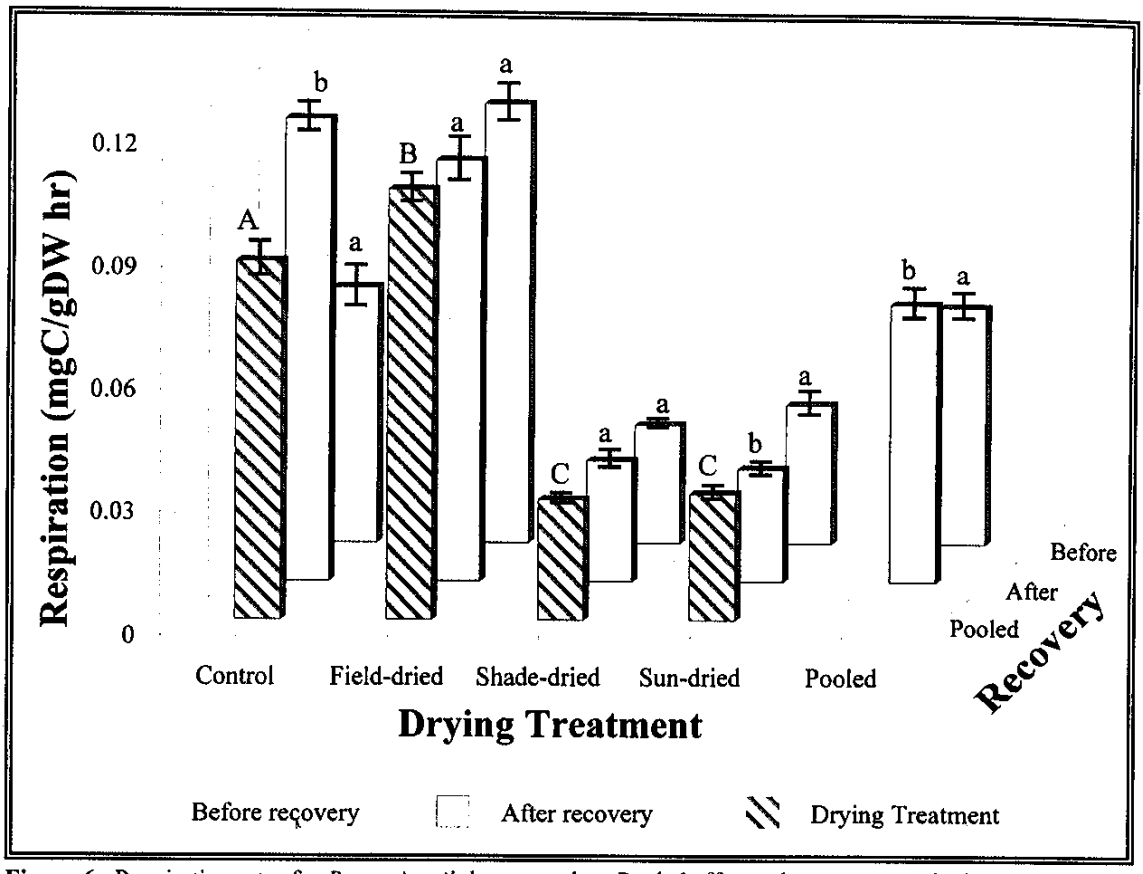

Figure 6. Respiration rates for *Bazzania trilobata* samples. Pooled effect values represent the impacts of the drying treatment or recovery period alone. Bars are means ± 1 s.e. Those with different letters are significantly different ($p < 0.05$). Upper case letters refer to the drying treatment effect; lower case letters refer to differences between treatments before and after recovery period.

indicating that photosynthetic pigment systems were functional. Analysis of variance indicated that gross photosynthetic rate differed significantly among treatments ($F=1607.04$, $p= 0.0001$) and before and after the recovery period ($F=53.47$, $p=0.0001$) (Appendix II). There was a significant interaction between treatment and recovery effects ($F=17.47$, $p=0.0001$).

Overall the highest gross photosynthetic rate occurred on control samples (Figure 7). Rates of the shade and sun-dried samples were equal and lowest, while those of the field-dried samples were intermediate. The pooled treatments showed higher gross photosynthesis

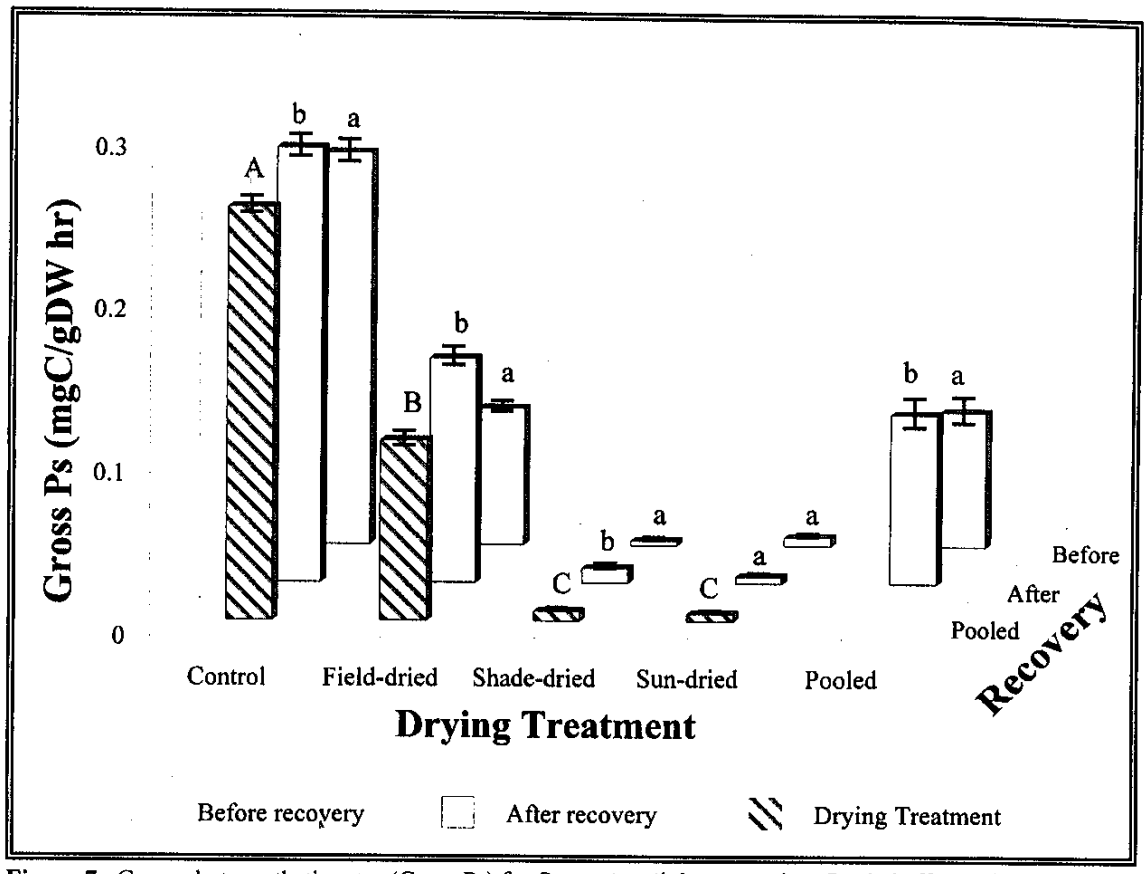

Figure 7. Gross photosynthetic rates (Gross Ps) for *Bazzania trilobata* samples. Pooled effect values represent the impacts of the drying treatment or recovery period alone. Bars are means ± 1 s.e. Those with different letters are significantly different ($p<0.05$). Upper case letters refer to the drying treatment effect; lower case letters refer to differences between treatments before and after recovery period.

following versus prior to the recovery period.

In terms of interactions (Figure 7), the control, field and shade-dried samples showed a significant increase in gross photosynthesis following recovery ($F=7.65$, $p=0.0071$; $F=69.95$, $p=0.0001$; and $F=13.42$, $p=0.0005$, respectively). There was no significant change in gross photosynthesis for the sun-dried samples following recovery.

Net photosynthesis. Only control and field-dried samples showed evidence of net photosynthesis, i.e. CO_2 gain (Figure 8). The net photosynthetic rate differed significantly among the treatments with the exception of the shade- and sun-dried samples ($F=1034.58$,

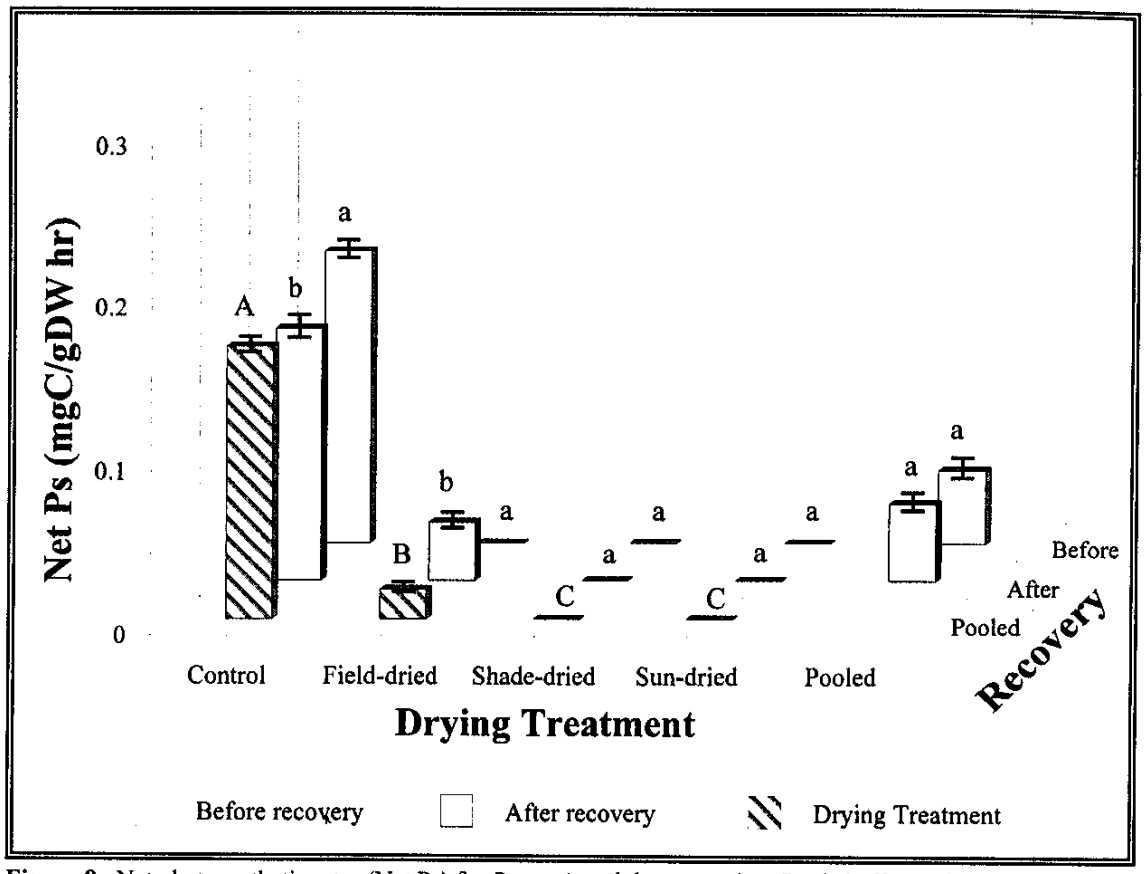

Figure 8. Net photosynthetic rates (Net Ps) for *Bazzania trilobata* samples. Pooled effect values represent the impacts of the drying treatment or recovery period alone. Bars are means ± 1 s.e. Those with different letters are significantly different ($p<0.05$). Upper case letters refer to the drying treatment effect; lower case letters refer to differences between treatments before and after recovery period.

p=0.0001, Appendix III). The difference in net photosynthetic rates of the pooled treatments before and after recovery was not significant (F=1.15, p=0.2835), but there was a significant interaction between treatment and recovery effects (F=24.96, p=0.0001).

Overall the highest mean net photosynthetic rate occurred in the control samples (Figure 8). Rates for the shade- and sun-dried samples were negligible and those for the field-dried samples were intermediate.

With respect to interactions, the mean net photosynthetic rate for controls decreased significantly following the recovery period (F=7.87, p=0.0063), whereas field-dried samples

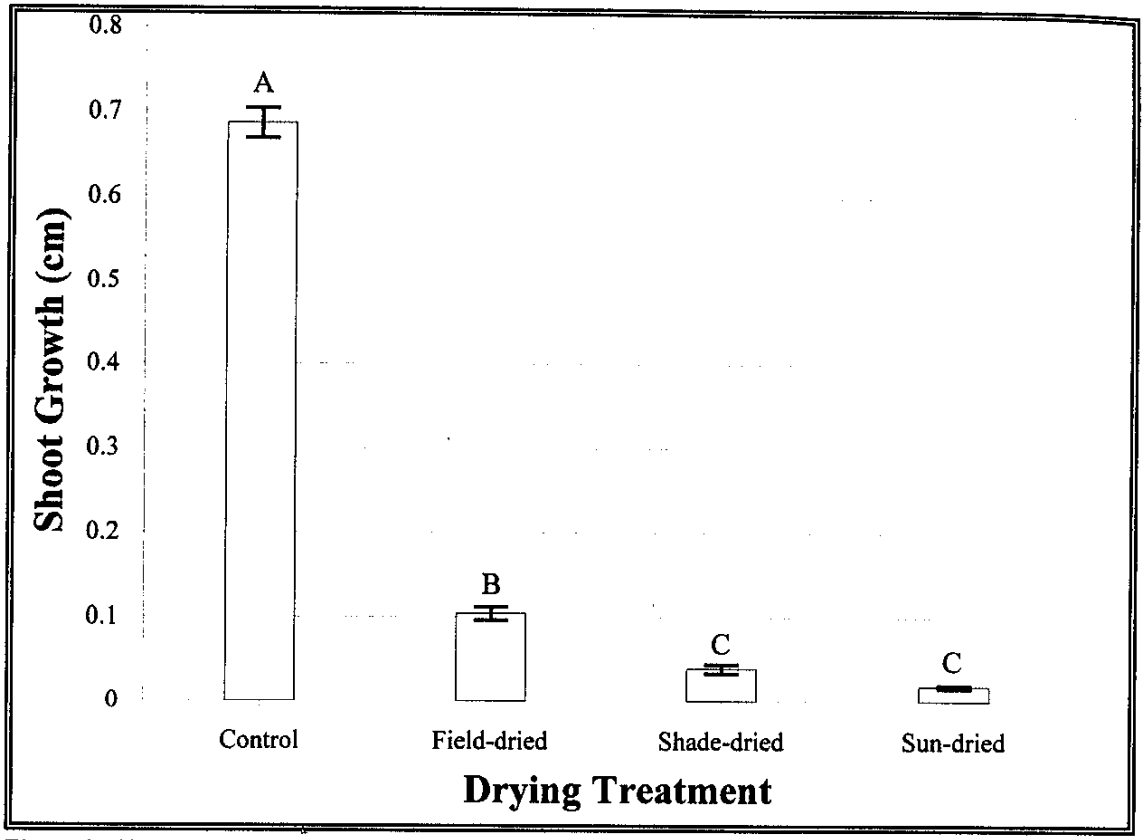

Figure 9. Shoot growth (elongation) during a two month recovery period for different treatments of *Bazzania trilobata* shoots. Bars represent means ± 1 s.e. Those with different letters are significantly different ($p<0.05$).

showed a significant increase following the recovery period ($F=61.58$, $p=0.0001$). There was no detectable change in rates for sun- and shade-dried samples.

Shoot growth

Mean shoot growth, measured as change in length, was significantly higher for the control group than it was for the other groups (Figure 9) ($F=1027.09$, $p=0.0001$, Appendix IV). Growth for samples from the clear-cut treatment was significantly greater than that for sun-dried and shade-dried shoots, both of which showed equal and negligible growth during the recovery period.

Following the recovery period, new branches and rhizoids were observed on shoots of

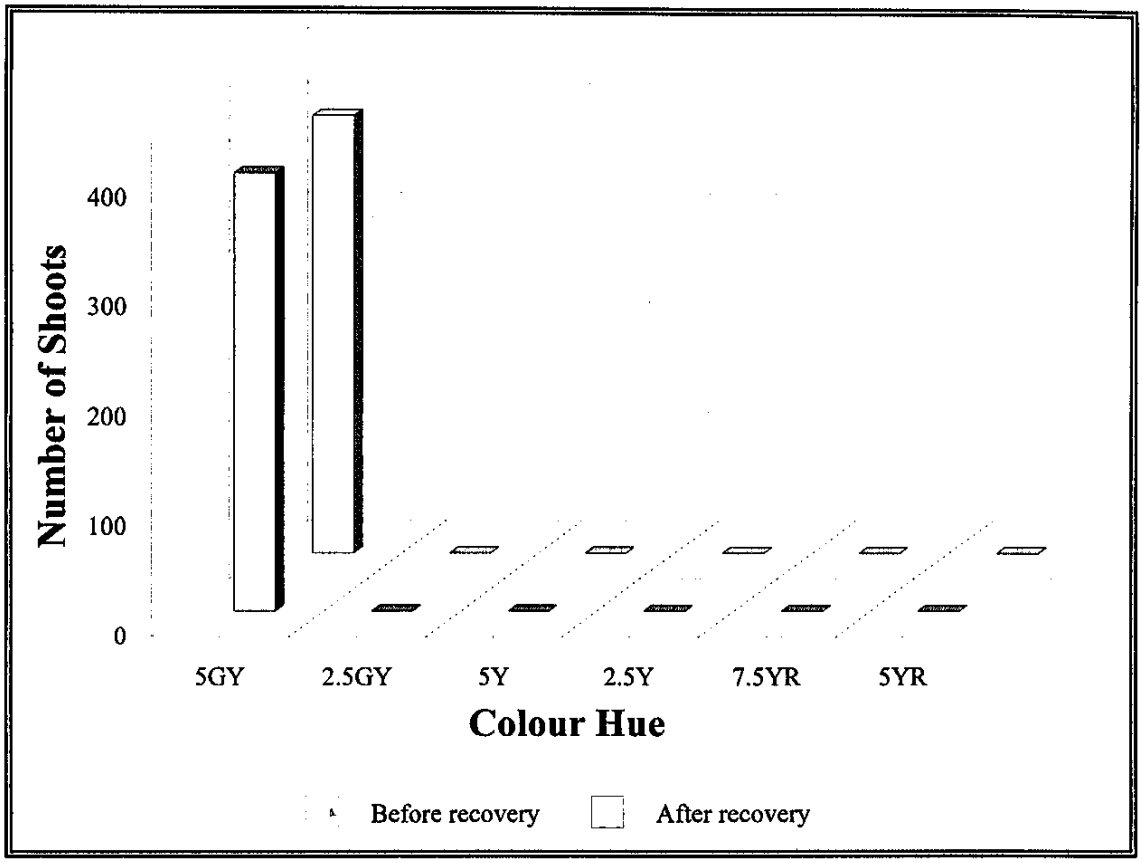

Figure 10. Control samples: Number of shoots (n=400) of *Bazzania trilobata* that fell into 7 colour hues as described by Wilde and Voigt (1977). Visual assessments were made before and after the 2 month recovery period.

the control group, and rhizoids were noted on many samples from the field-dried samples. Rhizoids and branching were not observed in the sun-dried and shade-dried shoots.

Colour assessment

The colour hue (*sensu* Wilde and Voigt 1977) of the control samples fell within the 5GY (green-yellow) range of the Munsell colour chart for all 400 shoots both before and after the recovery period (Figure 10). The other treatment groups all showed a shift in colour hue following the recovery period. The hue of the field-dried samples was predominately 5Y (yellow) at collection, shifting to 2.5 - 5Y and 2.5GY after recovery (Figure 11). The shade-

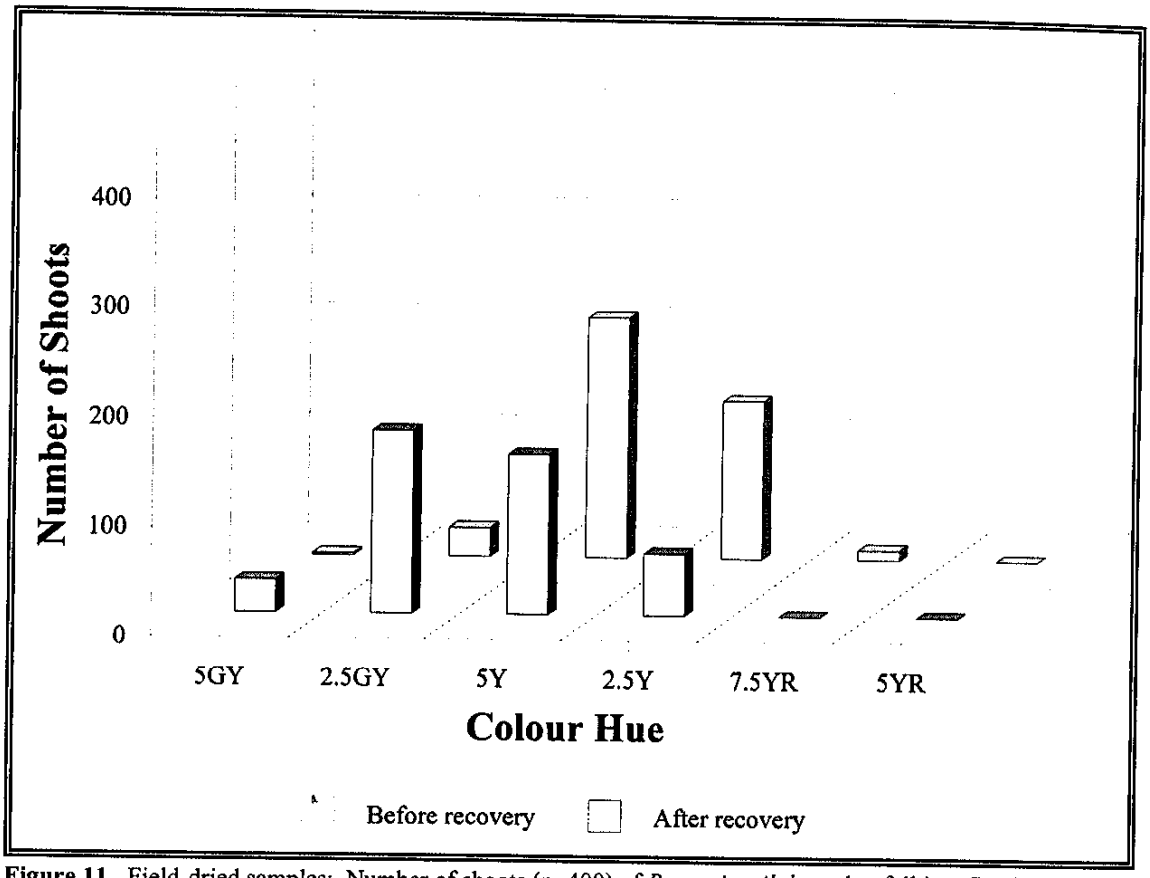

Figure 11. Field-dried samples: Number of shoots (n=400) of *Bazzania trilobata* that fell into 7 colour hues as described by Wilde and Voigt (1977). Visual assessments were made before and after the 2 month recovery period.

dried samples, which were similar to controls at collection, were predominately 2.5GY - 5GY after drying, shifting to 7.5YR and 2.5Y after recovery (Figure 12). The sun-dried samples shifted from a pre-regrowth hue ranging from 2.5Y to 5GY after drying to a post-recovery hue of predominately 2.5Y (Figure 13).

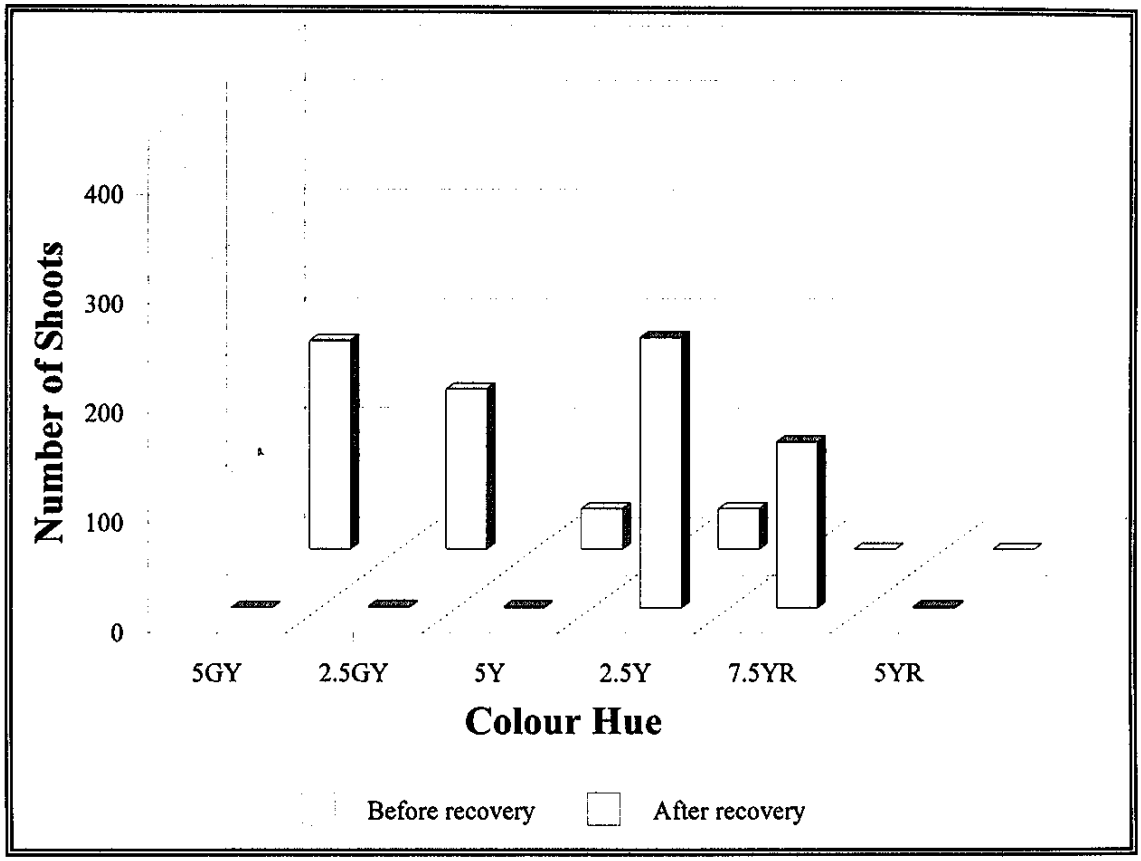

Figure 12. Shade-dried samples: Number of shoots (n=400) of *Bazzania trilobata* that fell into 7 colour hues as described by Wilde and Voigt (1977). Visual assessments were made before and after the 2 month recovery period.

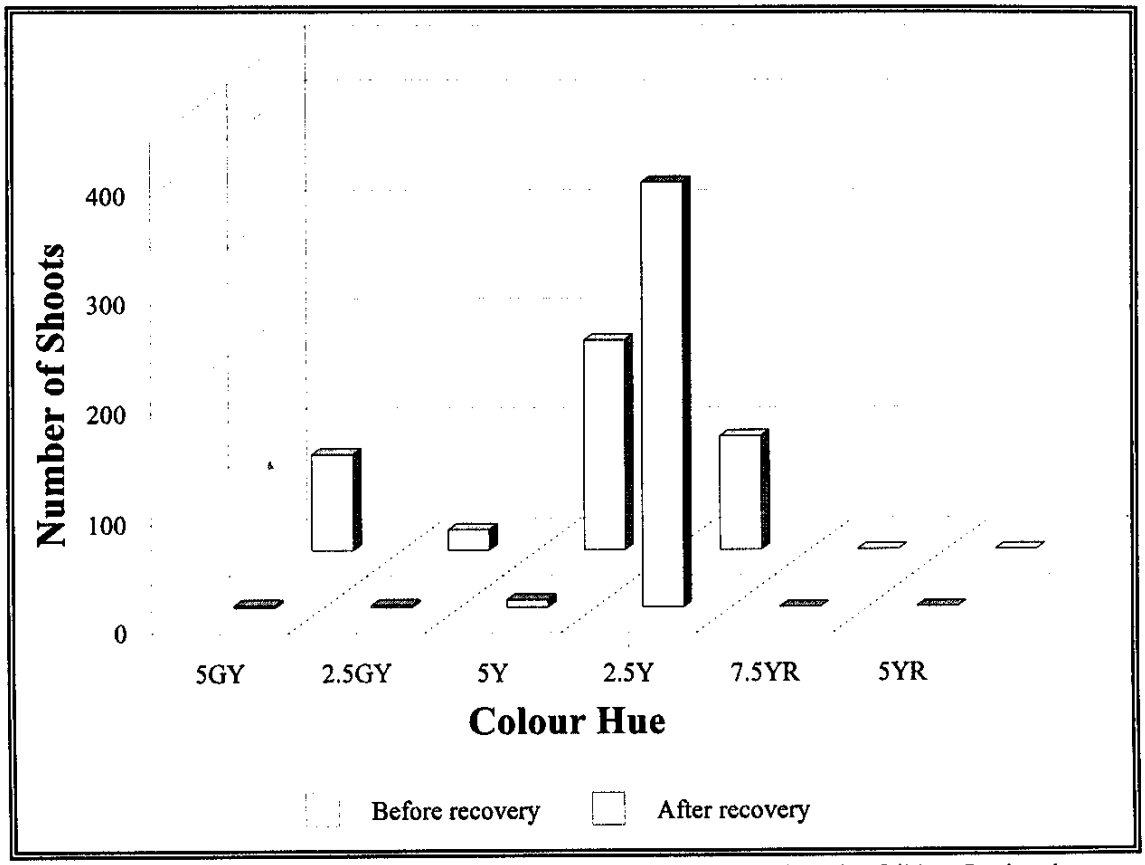

Figure 13. Sun-dried samples: Number of shoots (n=400) of *Bazzania trilobata* that fell into 7 colour hues as described by Wilde and Voigt (1977). Visual assessments were made before and after the 2 month recovery period.

DISCUSSION

Persistence of *Bazzania trilobata* following a forest disturbance depends on: (1) its ability to survive conditions following the disturbance, (2) regeneration of vegetative fragments, and/or (3) recolonization via spore germination from either persistent spore banks or neighbouring colonies. This study addresses only the first pathway to persistence: survivability. The ability of *B. trilobata* to recover following specific stresses was assessed using five measures: (1) respiration, (2) gross photosynthetic activity, (3) net photosynthetic activity, (4) shoot growth, and (5) colour change.

Based on respiration alone, it is clear that this liverwort can survive the stressful conditions following a forest clear-cut for at least two years. While its ability to recover under laboratory growing conditions has been demonstrated in this work, it remains to future studies to establish its ability to recover under field conditions.

Assessment of recovery

Infra-red gas analyses indicate that respiration, net photosynthetic and gross photosynthetic rates differ with drying treatment. The controls showed higher net and gross photosynthesis than the other treatments, lower respiration than the field-dried samples, and higher respiration than the remaining two treatments. This suggests that conditions in the buffer strip were different from three drying treatments, sufficient to alter metabolism significantly. In a closed forest such as the buffer, there is usually lower light intensity, more moderate temperatures, and higher and less variable humidity than in the clear-cut (Anderson and Hytteborn 1991; Rose 1992). Although the light intensity and temperature were much higher in the sun-dried treatment than they were in the shade-dried treatment, the two treatments did not differ from one another in metabolic parameters. This suggests that either

the presence/absence of light did not add stress or stresses were so great for both treatments that the effects of these two variables were overshadowed.

The impact of the recovery treatment alone is not relevant because it blurs the significant interactions which are central to the objective of this study. For example, although respiration of the pooled treatments differed before and after the recovery period, this was likely attributable to the large increase in the respiration of the control group after recovery. Similarly, net photosynthesis did not change overall after the recovery period, although rates for control and field-dried shoots varied in opposite directions.

The high gross photosynthetic rate of the control samples, relative to the other treatments, suggests higher metabolic activity. The low rate of respiration and higher net photosynthesis before recovery, relative to the field-dried shoots, suggest that samples from the closed forest (controls) were more robust than those from the clear-cut harvest area (field-dried). The high net photosynthesis implies that surplus energy and resources were available for growth. The greener colour of the controls relative to field-dried samples indicates the presence of healthy chloroplasts (Wilde and Voight, 1977) which supports the high photosynthetic values. This implies that conditions of the buffer strip were more favourable for *B. trilobata* than those of the clear-cut.

The large increase in respiration of the controls following the recovery period may be due to the use of carbon and ATP for (1) growth, and/or (2) repair (Raven *et al.* 1992). It is possible that the recovery conditions were less than optimal and therefore cellular repair was necessary. However, the increase in the net photosynthesis rate and shoot length, and the maintenance of colour, all indicate that growth occurred.

After two years in the clear-cut, respiration of *Bazzania trilobata* was clearly much higher and net photosynthesis much lower, relative to controls, indicating that conditions in

the clear-cut were very stressful. The shoots were viable, but all their energy was required for repair and maintenance, with negligible surplus for growth. However, the liverwort showed distinct signs of recovery. Following the recovery period, respiration remained high, but net photosynthesis increased significantly, suggesting that more energy was available for growth. The shift in colour, from yellow (damaged pigments) towards green (comparable to healthy, controls) indicated an increase in functional chloroplasts. In addition, allocation to growth was evident from observed shoot elongation. However, the post recovery field-dried shoots showed significantly less growth than the controls, which is consistent with their lower net photosynthesis. This suggests that a larger proportion of respiration was still allocated to cellular repair than occurs in healthy shoots. It would be interesting to track recovery over a longer period to determine the time required for field-dried shoots to attain the same health and vigour as control shoots.

None of the measures indicated significant recovery in the sun and shade-dried shoots. Although their colour was relatively closer to that of controls than was that of the field-dried shoots, green pigmentation declined further after the recovery period, and the three metabolic rates remained the same (very low) or declined. Shoot growth was so low (<0.1 cm) that it may be attributed to experimental error, and even the low rates of respiration and photosynthesis may be attributable to microscopic organisms such bacteria, fungi, or algae which may be present on the shoots (Schofield 1985). Future studies could investigate the presence and contributions of such factors.

Overall, it appears that the brief experimental drying regimes used on sun and shade-dried shoots were far more damaging, with less chance of recovery, relative to the conditions experienced in a clear-cut forest over two years.

Additional factors

The stress on *Bazzania trilobata* associated with drying treatments may have been compounded by aspects of the methodology. Physical removal of the shoots from the substrate and from each other may disturb endogenous fungi. These fungi, which often occur in stems of the liverwort, are thought to be important in nutrient and moisture uptake (Schofield 1985). Removal from the colony may have disturbed such symbiotic relationships which in turn may have caused a decline in vigour of the liverwort (Brown and Bates 1990).

In addition, the ability of the shoots to trap water was presumably altered when the physical structure of the colony was disturbed. Colonial architecture is known to strongly affect water absorption and retention in bryophytes (Proctor 1982; Schofield 1985). Bryophyte mats often hold 5 to 10 times their dry weight in water, most of which is held in extra cellular spaces (Proctor 1982). The experimental design required that the shade-dried and sun-dried samples spend a greater amount of time separated from the densely packed colonies than did the control or the field-dried samples. This almost certainly increased both total water loss and the rate of dessication. Metabolic activity in bryophytes is opportunistic and strongly related to the hydration level, so dessication affects respiration and photosynthetic rates (Gerdol *et al.* 1996). In addition many bryophytes are better able to tolerate dessication if it occurs gradually (Schofield 1985). The field dried shoots were presumably rehydrated occasionally, by dew and precipitation, unlike the other dried shoots. This rehydration may have increased the survivability of the field-dried shoots (Proctor 1982).

Recovery and regeneration of shoots

This study indicates that *Bazzania trilobata* can recover from stresses related to clear-

cut harvesting, given a period of favorable conditions for recovery. Although the conditions imposed during experimental drying (shade-dried and sun-dried) were beyond the range of tolerance for *B. trilobata*, as indicated by the lack of metabolic activity following the recovery period, it is not known exactly what the critical conditions are, nor how long the plants can tolerate these conditions. The time required for forest regeneration to provide a range of conditions favourable for the recovery *B. trilobata* is also unknown. As a result, we cannot predict whether the regenerated forest floor will ultimately contain this species from persistent colonies.

The species may, however, regenerate by other mechanisms. After approximately 1 month of the recovery conditions, the substrate of the field-dried samples was uniformly covered with tiny plants which appeared to consist of only one leaf. They must have developed from spores that were present either in the substrate or on the shoots at the beginning of the recovery period. Although the substrate on which all samples were grown was taken from the same source (decayed wood from the buffer strip), these tiny plants were not observed growing on the substrates associated with the other drying treatments.

While one might speculate that spores of *B. trilobata* were present on all samples and in the substrates, but only germinated in those treatments where there was less competition for resources, this does not explain the absence of plantlets from the sun- and shade-dried treatments. It is known that spore germination is moisture and temperature dependant (Schofield 1985). The robust control samples may have consumed so much of these resources that conditions were not appropriate for spore germination, but all treatments had the same temperature and moisture conditions during recovery. No plantlets grew in the sun- and shade-dried samples even though competition there was less than for the field-dried samples.

A more plausible explanation is that samples from the open, windy clear-cut may have received a wide variety of airborne spores, including those of pioneer species, that do not reach sheltered forest sites. Future studies should culture these plantlets to determine whether they are *B. trilobata* or another bryophyte.

Biodiversity

Concern for the maintenance of native biodiversity provided the motivation for this study. The implications of ranges of environmental tolerance for one species may be far-reaching, as the loss of one species can result in the loss of habitat for other species (Myers 1995). Although colonies of *Bazzania trilobata* were present in both the clear-cut area and the buffer strip, this study showed that shoots in the buffer strip were healthier. It is assumed that differences in environmental conditions between the forest and the clear-cut were responsible for the differences the health of the specimens.

It is beyond the scope of this study to determine the impact of the changes in environmental conditions on closely associated species. It is possible that species which have symbiotic relationships with *B. trilobata* or which have narrower ranges of tolerance for environmental conditions may experience adverse effects following a clear-cut disturbance. Several qualitative differences in the two communities suggest that the condition of *B. trilobata* may be related to the survival of other species. Toads, snakes and spiders were observed on and within the colonies of *B. trilobata* found in the buffer strip. These were absent from colonies found in the clear-cut area; instead, ants were observed in these colonies.

These observations also highlight the importance of the buffer strip as a refuge. The range of environmental conditions under the closed canopy are different than that of the clear

cut area and allow for a different combination of species.

Bazzania trilobata as an indicator species, and future research

The abundance, ease of visual identification, and sensitivity to dessication (including changes in light intensity and humidity associated with canopy removal) of *Bazzania trilobata* may make it a useful indicator for a specific range of environmental conditions, and the status of species associated with those conditions. More information is required, however, to refine the use of *B. trilobata* as an indicator. The exact range of its tolerance to environmental conditions must be determined, including temporal aspects. Further studies should determine the extent of recovery in the field, e.g. clear-cut areas of different ages could be inspected for signs of recovering *B. trilobata*. The ranges of tolerance of closely associated organisms could also be determined, to identify those which fall within the same range as *B. trilobata*.

The colour shift from yellow to green which occurred for the field-dried samples during the recovery period suggests that colour may be an indicator of the metabolic activity of *B. trilobata*. It must be noted, however, that colour analysis of the shade-dried and sun-dried samples prior to recovery indicated green shoots, while net and gross photosynthesis were nil, and respiration was very low. While further infra-red gas analysis of shoots may provide a correlation between colour and metabolic activity, consideration must also be given to additional factors.

Although it was not quantified in this study, many of the experimentally-dried samples were observed to be brittle in texture, even when green. This suggests that assessment of both texture and colour may be necessary to indicate the metabolic status of *B. trilobata*.

Future studies should also compare colonies with isolated shoots of *B. trilobata*, to determine the relevance that colonial architecture has to water relations, and thus to tolerance. Metabolic activity of organisms which are epiphytic on *B. trilobata* should also be determined, to isolate the CO_2 metabolism attributed to the liverwort.

Conclusions

This study indicates that *Bazzania trilobata* is a potentially useful indicator of environmental conditions associated with mixed forests in New Brunswick. This leafy liverwort is easily identified in the field, even by non-bryologists. Robust and abundant patches of *B. trilobata* are commonly found in a variety of forest habitats, the common elements of which are low light intensity and high humidity. This study has shown that *B. trilobata* is sensitive to dessication, and experiences morphologic and metabolic changes following dessication. These changes include: (1) shift in colour from green to yellow as bleaching and dessication occur, (2) decline in metabolism, and (3) differential ability to recover after a return to favorable conditions. Shoot growth and increase in metabolic activity following the recovery period provide evidence that field-dried samples remained viable until environmental conditions improved.

Shade-dried and sun-dried samples were exposed to conditions outside the range of tolerance for the species and experienced reduced metabolic activity and colour change from which they did not recover. As expected under such conditions, mean shoot growth was negligible.

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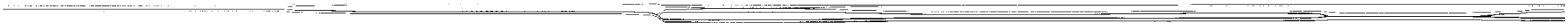
APPENDICES

APPENDIX I. Analysis of variance comparing mean respiration rates with respect to the main effect of drying treatments, recovery and interaction of treatment/recovery period before and after the recovery period for *Bazzania trilobata*. The four treatment types are: control, field-dried, shade-dried and sun-dried (n for each = 40).

Source	DF	Sum of squares	Mean square	F value	P value
Treatment	3	0.3656	0.1219	237.29	0.0001
Recovery	1	0.0079	0.0079	15.38	0.0001
Treatment X Recovery	3	0.0450	0.0150	29.20	0.0001
Error	312	0.1602	0.0005		
Total	319	0.5788			

APPENDIX II. Analysis of variance comparing mean gross photosynthetic rates with respect to drying treatments, recovery and interaction of treatment/recovery before and after the recovery period for *Bazzania trilobata*. The four treatment types are: control, field-dried, shade-dried and sun-dried (n for each = 40).

Source	DF	Sum of squares	Mean square	F value	P value
Treatment	3	3.3343	1.1114	1607.04	0.0001
Recovery	1	0.0370	0.0370	53.47	0.0001
Treatment X recovery	3	0.0362	0.0121	17.47	0.0001
Error	312	0.2158	0.0007		
Total	319	3.6233			



APPENDIX III. Analysis of variance comparing net photosynthetic rates with respect to drying treatments, recovery and interaction of treatment/recovery before and after the recovery period for *Bazzania trilobata*. The four treatment types are: control, field-dried, shade-dried and sun-dried (n for each = 40).

Source	DF	Sum of squares	Mean square	F value	P value
Treatment	3	1.5538	0.5179	1034.58	0.0001
Recovery	1	0.0006	0.0006	1.15	0.2835
Treatment X recovery	3	0.0375	0.0125	24.96	0.0001
Error	312	0.1562	0.0005		
Total	319	1.7481			

APPENDIX IV: Analysis of variance comparing shoot growth (cm) among four treatments of *Bazzania trilobata*. The four treatment types are: control, field-dried, shade-dried and sun-dried. (n for each = 400).

Source	DF	Sum of squares	Mean square	F value	P value
Treatment	3	121.7647	40.5882	1027.09	0.0001
Error	1596	63.0702	0.0395		
Total	1599	184.8350			