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Fundy Model Forest Report 2000

Potential refugia for forest floor bryophytes: remnant canopy and riparian buffers

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Summary

Many forest floor bryophytes (mosses and liverworts) are unable to survive forest harvest. Because the distribution of many species is believed to be limited by dispersal, conservation of moss and liverwort diversity in managed forest landscapes requires the presence of refugia (areas within harvested stands where populations can survive). This project expanded on the pre- to post-harvest monitoring program established in the Hayward Brook Watershed study area and evaluated two potential refugia: areas within the clearcut with remnant canopy and no forest floor damage, and riparian buffer zones.

Compared to areas where the forest floor was damaged by machinery, remnant canopy that experienced no damage to the forest floor, were more similar to the pre-harvest bryophyte community. Subtle differences in the environment and in the bryophyte community beneath different heights of remnant canopy were also found. While remnant canopy patches less than 1.5m in height resulted in a microclimate measurably different from the clearcut, remnant canopy patches greater than >1.5m in height contained the bryophyte community most similar to the pre-harvest community.

Riparian buffer zones contained some of the bryophyte species of the pre-harvest community including two species which did not survive forest harvest in the adjacent harvested areas. However, the bryophyte community in the riparian buffer was measurably different from the pre-harvest bryophyte community and contained many species which were not found in the pre- or post-harvest communities of the adjacent cutblocks. This indicates that while the buffer has some potential as a refugium, it is not as effective as remnant canopy and contains a distinct community which may be at risk if it is subjected to partial harvesting.

We conclude that maintenance of forest floor bryophyte diversity would be enhanced by: (1) reduction of the area of machinery tracks, and (2) retention of patches of remnant canopy >1.5m in height, and (3) restricted or careful logging of buffers.

Potential refugia for forest floor bryophytes: remnant canopy and riparian buffers

General Introduction

New Brunswick forests are predominantly managed for tree harvest; for example, 30.5% of forested land was clearcut between 1975 and 1995 (CCFM 1997). As a result, natural disturbance regimes at the forest stand and landscape scales are replaced by a disturbance regime created by forest management. This extensive style of management creates a fragmented landscape in which the continuity of the forest landscape is broken by harvested and other disturbed areas. Fragmentation, while frequently used with reference to fragments of forest within an agricultural matrix (e.g. Saunders et al. 1991), also applies to any break in a habitat that impedes movement of species (Fahrig and Merriam 1994). While a landscape of harvested and unharvested stands may not be perceived as fragmented by mobile and long-lived species (e.g. many vertebrates), harvested and managed stands may fragment the landscape for dispersal limited short-lived organisms (e.g. many epixylic bryophytes). Landscape fragmentation, along with the inherent habitat change associated with forest harvest, presents a threat to many species which are unable to reach territory required for part of their life cycle (e.g. different breeding and feeding habitats of birds, or amphibians Waldick 1994), or whose offspring cannot reach new habitat patches (Fahrig and Merriam 1994).

The amount and rate of fragmentation may affect the forest floor bryophyte community. Several studies have indicated that bryophytes may be dispersal limited (Söderström 1987, 1988, Herben et al. 1991, Söderström et al. 1992). A model developed by Herben et al. (1991) indicated that available substrate in a clumped pattern increased survival of populations of the moss *Orthodontium lineare*. This suggests that the dispersal distance from the parent plant or source population to the available habitat may be the limiting step to colony establishment. Our monitoring work established that many forest floor bryophytes are unable to survive forest harvest either due to physical damage and/or microclimatic change. A fragmented landscape with increased dispersal distances may therefore threaten the survival of forest floor bryophytes (Frisvoll and Prestø 1997, Rambo and Muir 1998). Further, the rate of landscape change may be a greater threat to species survival than degree of fragmentation (Fahrig and Merriam 1994). If forest floor bryophytes are unable to disperse from one suitable habitat to the next within the rotation time of a cut block, local population extirpation may lead to regional extirpation.

The most effective way to promote bryophyte survival across the landscape may be to conserve populations within harvested stands thus minimizing dispersal distances to, and re-colonization times of, harvested areas. In order to function as refugia these areas (1) must not experience extreme microclimatic changes associated with clearcuts such as increased incident photosynthetically active radiation (PAR), temperature and decreased humidity, (Nyland 1996) and (2) must contain forest floor bryophyte species at risk. This project was undertaken in two parts: Part 1. Patches of remnant canopy left in clearcuts as refugia, and Part 2. Riparian buffers as refugia. Part 3 provides a general discussion and our recommendations.

Part 1: Remnant canopy as refugia

Introduction

Forestry creates a heterogenous pattern of disturbed forests on the landscape and within stands. Clearcutting [the dominant form of stand harvest in New Brunswick (CCFM 1999)] does not always entail the complete removal of all trees within a stand. Advanced regeneration (young trees of merchantable species), Ahabitat@ or Awildlife@ trees (large trees left as habitat for cavity-nesting birds) and Aseed@ trees (usually large *Pinus* spp.) may be left intact. As a result, harvested stands are composed of areas that either: (1) have been run over by machinery or buried under tree limbs and twigs deposited as slash leaving no remnant canopy, or (2) have not been run over and may have some remnant canopy composed of advanced regeneration and habitat or seed trees. The effect of such heterogeneous disturbance on plants may be described within the context of disturbance theory. For this report, the broad definition of disturbance used by White and Pickett (1985) was modified to include direct disturbance in which plants are physically damaged (e.g. crushed on machinery tracks), and indirect disturbance in which the environment is changed, e.g. canopy removal results in altered temperature and humidity regimes (Saunders et al. 1991, Nyland 1996). These two types of disturbance incorporate suites of variables that may trigger different responses in the bryophyte community. Direct disturbance on machinery tracks destroys all or most of the community (Peterson 1999). Indirect disturbance, such as microclimatic change within patches of advanced regeneration, will apparently result in a less abrupt and less complete change in the forest floor bryophyte community (Fenton 2001, Peterson 1999). Busby et al. (1978) demonstrated the microclimatic sensitivity of bryophytes by documenting the reduction in their growth rates when the shrub layer or the entire canopy was removed.

The results of previous studies (e.g. Peterson 1999) suggested that the resultant bryophyte communities in areas which experienced direct and indirect disturbance were different. This study was designed to test this suggestion, and to examine the environment associated with each disturbance type. It predicts that: (1) differences in forest floor bryophyte survival may be related to differences in the environment in areas which experienced direct vs indirect disturbance and (2) differences in indirect disturbance severity result in a gradient, where those patches that had the most canopy removed experienced (a) the most severe microclimatic alterations and (b) the greatest resultant change in the bryophyte community.

Methods

Study site

This study took place within the Hayward Brook Watershed, New Brunswick in the Acadian mixed forest region. The stands used in this study had been predominantly *Abies balsamea* and *Picea* spp. before they were harvested in fall 1995 by the landowner, J.D. Irving Ltd, according to its standard operational plan. Advanced regeneration (young trees of merchantable species), non-merchantable trees (many species of any age with low market value), wildlife trees and seed trees were left standing in strips, generally 10m wide, between tracks made by machinery (e.g. feller-bunchers and skidders). Patches within these strips were classified as one of seven disturbance classes by type and severity of disturbance representing a proposed disturbance severity gradient. Four tree height classes, which experienced indirect disturbance, were: tall (trees >5m in height), medium (1.5-5m), low (<1.5m), and open (no canopy and no substrate disturbance). Direct disturbance classes were: substrate disturbed (substrate disruption or < 80% slash), slash-pile (>80% slash), and skidder (substrate compression and disruption).

Transect placement

In 1999, eleven transects were placed through randomly chosen 50 metre sections of remnant canopy strips (indirect disturbance) according to the following criteria:

(1) pre-harvest canopy was dominated by coniferous trees - determined by examining the stumps present, and composition of the litter below the surface leaf layer,

(2) no anthropogenic substrate disturbance was evident, and

(3) transect passed through a minimum of at least 5 m of each of two tree height classes.

Transects were also chosen to balance the number of patches of each disturbance class across the samples, and to represent the entire study area. Locations of skidder trails and transect ends were entered into a GIS database using a Trimble F\GeoExplorer Global Positioning System unit. Positions of harvest blocks, roads, and streams as well as elevations were obtained from the GIS databases of the Fundy Model Forest and J.D. Irving, Ltd.

The eleven transects ranged from 13 to 20 metres long, and 67 to 87 metres in elevation. Distance from the road ranged from 14m to 292m, while distances from the streams ranged from 45m to 286m (Figure 1 and Table 1).

Data collection

Three sets of data were collected:

(1) structural characteristics of tree height classes - frequency of trees and a sample of heights and diameters,

(2) microclimate of remnant canopy patches - temperature, relative humidity, PAR and precipitation, and

(3) % cover of substrates, trees, herbaceous plants, and bryophytes.

(1) Structural characteristics of tree height classes.

For each tree height class through which a transect crossed, the frequency of each species of tree present was recorded. Heights and basal circumferences were measured for ten randomly selected trees in each of the <1.5m, 1.5-5m and >5m height classes. Heights of trees less <3m tall were measured with a tape measure, while those for trees of 3-5m were estimated. Because it was not possible to determine the height of trees >5m tall, they were assigned an arbitrary height of 8m. The area of each canopy class was measured, and tree density and total basal area per square metre were calculated.

(2) Microclimate of tree height classes.

Data-loggers recorded temperature, relative humidity and photosynthetically active radiation (PAR; light of wavelengths which can be used in photosynthesis) in the four tree height classes and the open clearcut (control) using probes 207, HMP45C, and L190SB respectively (Campbell Scientific, Logan, Utah). Incident precipitation was collected in rain gauges and recorded in ml. Because rodent damage to probe wires resulted in lost data for data collected June - September 1999, data were also collected April - September 2000.

One set of probes (one temperature/ relative humidity probe and one PAR probe) was placed in a representative of each tree height class. Two dataloggers were rotated through four Areplicates@ of each tree height class at weekly intervals to capture seasonal variability (Figure 2). A third data-logger, used as a reference (control), was placed in a completely open (tree-less) area of the clearcut and was not moved. Temperature, relative humidity and PAR density (ì m/s$\$m^2$; a measure of photon density) were recorded as hourly averages, as well as daily maxima and minima. In 2000, PAR was also recorded as hourly and daily totals (mmoles/m^2; total number of photons received).

(3) Environmental features and bryophyte community patterns.

Each transect was sampled using contiguous 0.5 x 0.5m quadrats from one machinery track through remnant canopy to another machinery track (Figure 2). In each quadrat the percent cover of canopy, available substrates (forest floor not colonized by bryophytes), and bryophytes was measured.

Each quadrat was assigned to a disturbance class, i.e. one of: skidder trail, slash, substrate disturbed (direct disturbance); open, low, medium, or tall (indirect disturbance). Percent covers of all trees, non-woody vascular plants and available substrates (Table 2) were recorded for each quadrat.

Variables that document disturbance were also measured: (a) skidder trail - % cover of the quadrat on a skidder trail and (b) slash - % cover of bark, twigs, fine and coarse woody debris originating from the tree harvest. As these overlap with available substrate, they were analysed separately to avoid auto-correlation.

Because litter accumulation (either needle or deciduous leaf) may impact the bryophyte community, depth and dominant component of the plant litter, were measured and averaged at four points within each quadrat. In order to approximate the amount of incident PAR received by each quadrat, a reading of incident PAR was taken at four points within each quadrat as it was sampled (LI-185A quantum/ radiometer/ photometer Li-Cor; Lincoln, Nebraska).

Within each 0.5 x 0.5m quadrat, percent cover and substrate were recorded for all bryophyte species, including those on slash up to 1m above the surface of the quadrat and on trunks up to 0.5m. Voucher samples were collected for identification in the laboratory and remain in the herbarium at the University of New Brunswick, Saint John. Taxonomy follows Ireland (1982) and Crum and Anderson (1981) for the mosses and Schuster (vols II-IV 1969, 1974, 1980) for the liverworts.

Analyses

(1) Microclimatic data. Relative humidity was converted to vapour pressure deficit (VPD; a temperature-relevant measure of humidity) by the following formula:

$$VPD = (6.1078)*\{exp[17.269*T/237.3+T)]\}*(1-RH)$$

where T is temperature in Celsius, and RH is relative humidity as a decimal (modified from Tanner 1972).

To examine the pattern of PAR density, temperature and VPD over the course of the sampling period, values recorded in each disturbance class were averaged for each sampling period (one to three weeks) and plotted against time.

Values of mean, maximum and minimum for total daily PAR, PAR density, temperature, and VPD were calculated for each disturbance class. Because species may be limited by extreme, rather than mean, microclimatic conditions, frequency distributions were plotted for total daily PAR, PAR density, temperature, and VPD within each disturbance type. Total daily PAR of each disturbance class was expressed as percent of total control PAR for the same day. To address the potential impact of the surrounding vegetation on the amount of PAR reaching the forest floor in the open tree height class, it was divided into two sub-categories: open adjacent to a machinery track, and open surrounded by other tree height classes.

All values of PAR density, temperature, and VPD from all disturbance classes over the sampling season were divided into 10 percentile groups (i.e. ranked and divided into ten groups with equal numbers of data points). Then, percent frequency of percentiles was calculated by disturbance class. The 10 percentile groups were further grouped into 5 pentile groups for ease in graphing.

In order to evaluate co-occurrence of high or low PAR density, temperature and VPD values, a microclimatic index was calculated. Hourly values of PAR density, temperature, and VPD that fell within the range of the lowest 10% of data points was assigned an index value of 1, values which fell in the range of the second lowest 10% of data points was assigned an index value of 2, etc. The index values of PAR density, temperature and VPD for each hour were summed and divided by 3. The microclimatic index, therefore, ranges from 1 (1st percentile of PAR density, temperature, and VPD) to 10 (10th percentile of PAR density, temperature, and VPD).

(2) Environmental features and bryophyte data. The programs PC-Ord (McCune and Mefford, 1999), and Canoco 4 (ter Braak and Šmilauer, 1998) were used to perform multi-variate analyses. Multi-response permutation procedure (MRPP) was used to compare disturbance classes using: (a) environmental and (b) species data. Four diversity indices were calculated for each quadrat using PC-Ord (McCune and Mefford 1999): total bryophyte cover, richness, evenness, and Simpson=s Diversity Index, which emphasizes dominant species rather than rare species (Krebs 1989). One-way analysis of variance (ANOVA) and Tukey=s test were used to compare the individual variables (e.g. mean patch area, total bryophyte cover) among disturbance classes. Variables that did not have homogenous variances were analyzed using the Kruskal-Wallis test. In order to correct for the dominance of low values in total bryophyte cover, it was log-transformed before analysis.

Quadrat values for litter depth, litter ratio (needle: leaf), and readings of PAR were ranked and tested for differences among disturbance classes using Kruskal-Wallis tests.

Detrended canonical analysis (DCA) was used to explore the species and quadrat patterns. Environmental variables and quadrats with less than five species were passively inserted into the pattern (Økland 1990). Pearson=s correlation coefficient was used to test relationships between DCA scores of the quadrats and environmental variables. In all tests, Æ=0.05 was used.

Results

Description of the bryophyte environment

(1) Structural characteristics of tree height classes

Remnant canopy patches differed in a number of characteristics (Table 3). Mean tree heights differed among tree height classes, as would be expected. Tall patches were also significantly larger than medium, low or open patches, with a mean size of 37m^2. Although the differences were not significant, tree density tended to increase with decreasing height. Basal area, which reflects not only the number of trees but also their size, differed among the classes, from 43 cm^{2}m^{-2} in tall to 8 cm^{2}m^{-2} in low. In terms of composition, medium and low patches were dominated by *Abies balsamea* (66% and 75% respectively), whereas tall patches contained mixtures of *Picea* spp. (42%) and *Abies balsamea* (45%).

(2) Microclimate of tree height classes.

The means and extremes of incident precipitation, PAR, temperature and VPD experienced by the bryophyte community differed among tree height classes. The total and mean amount of precipitation received by tree height classes was inversely correlated with height of trees (Table 4). Over the course of the sampling period, temperature and VPD increased in the control (open clearcut) until mid-August when temperature began to decrease (Figure 3). VPD remained high until the end of the sampling period. Density of incident PAR in the control patch peaked in June, and gradually declined over the remainder of the sampling period. Open patches differed from the pattern described for controls only in that both temperature and VPD declined in mid-August, and the decrease in incident PAR density after June was more pronounced. Temperature and VPD in the tall, medium, and low patches increased gradually to a peak in July and early August. Density of incident PAR declined rapidly in late April and early May in the tall patches as the deciduous trees leafed out, while incident PAR density in the low and medium patches peaked in June and declined over the remainder of summer.

Overall, the means and ranges of PAR density, VPD and temperature of tall, medium and low classes were similar, while the open class had values intermediate but nearer to control (Table 4).

Values of total daily PAR in disturbance classes varied from < 5% to 91% of control. Approximately 90% of total daily PAR values recorded in tall, medium and low patches were <10% of the control (Figure 4). In contrast, almost 80% of total daily PAR values in open patches surrounded by canopy were 21- 50% of the control and 50% of total daily PAR values recorded in the open-edge patches were >50% of the control with 20% reading 80-100% of control.

The density of incident PAR in disturbance classes ranged between 0 and 2063 ìms^{-1}m^{-2} (Table 4). During the sampling period 80% of the PAR density received by tall, medium and low patches was less than 32 ìms^{-1}m^{-2} (Figure 5). However, tall patches had a higher frequency of incident light between 32 and 149 ìms^{-1}m^{-2} than did medium or low patches. Open and control patches both predominantly received incident PAR that was > 32 ìms^{-1}m^{-2} , and in control, 46% were >149 ìms^{-1}m^{-2} .

Vapour pressure deficit (expressed as a percentage) in disturbance classes varied between 0 and 96% (Table 4). VPD in tall patches was generally < 5 %; VPD >12 % was experienced during < 20% of the sampling period (Figure 5). Medium, low, open and control patches experienced VPD > 12 during 40-50% of the sampling period.

Temperatures ranged from - 6^{0}C in late April to 46^{0}C in late August (Table 4). Mean temperature and the frequency of temperatures above 22^{0}C increased from tall through medium to low patches (Table 4, Figure 6). Open patches were warmer than tall, medium and low patches, and cooler than control. The control patch had a higher frequency of extreme temperatures, i.e. >22^{0}C, and < 9^{0}C.

All disturbance classes had similar frequencies of low microclimatic index values. The frequency of high microclimatic index values increased from tall to control through medium, low, and open patches (Figure 6).

(3) Fine scale pattern of substrates and canopy.

Overall, the environment differed among the disturbance classes in both substrates (forest floor) and local herbaceous canopy. The percent cover of available substrates differed significantly among all disturbance classes with the exception of skidder versus substrate disturbed and open versus substrate disturbed (Table 5, upper right). The herbaceous layer differed significantly among all classes except for medium vs low ; low vs open; and, open vs substrate disturbed quadrats (Table 5, lower left). Considering both local canopy and substrates, only the open and substrate disturbed quadrats were not significantly different ($T = 0.152$; $p = 0.4639$).

Differences in percent cover of individual substrates (Table 6) illustrate the presence or absence of substrate disturbance (and therefore direct disturbance). Percent covers of bare mineral soil and humus were ten and two times greater in the quadrats that had experienced substrate disturbance (skidder and substrate disturbed classes, respectively). Percent cover of roots and rocks were two times higher on the skidder trails, reflecting mechanical damage to the forest floor. Twigs and woody debris had the highest values (30 and 43% respectively) in slash-piles, as would be expected. Open and substrate disturbed quadrats had 24 and 26% cover of woody debris, as slash occasionally was deposited in these areas. Frequent available substrates in the tree height class quadrats included trunks and needles, values of which peaked at 2% and 53% (respectively) in tall quadrats and declined to 0% and 22% in open quadrats.

Overall, the number of available substrates (substrate richness; Table 6) was significantly greater in the tall and low quadrats than in the slash-pile quadrats; other disturbance classes had intermediate levels of substrate richness.

The litter of all classes was dominated overall by needles (Table 7), although tall, open, and substrate disturbed had higher levels of leaves than medium, or low. Litter was deepest in the tall and medium quadrats (14mm and 12mm respectively).

Disturbance classes differed in canopy cover at the quadrat level. Total tree cover was highest in the medium quadrats (Table 8) but did not differ significantly from tall or low quadrats. Total herbaceous cover was greatest on the skidder trails, potentially reflecting the increased exposure of the soil seed bank and higher incident sunlight. Of the tree height classes, open quadrats had the highest total herbaceous cover.

Means of the four readings of incident PAR per quadrat were ranked (lowest value of PAR = lowest rank). The rank of the of PAR increased with decreasing canopy cover (Table 8).

Description of the bryophyte community

(1) Overall description

Overall 93 species, comprising 68 mosses and 25 liverworts, were found in 363 quadrats (Appendix 1). Twenty-five species (14 mosses and 11 liverworts) were found only in remnant canopy patches, and seven of these (four mosses and three liverworts) had been recorded as Alost@ from permanent quadrats after harvest in an associated study (Hayward Brook Watershed - permanent quadrats). Nineteen species, including seven liverworts, were found only in quadrats with remnant tree canopy (tall, medium or low). In total, 25 species were added to the cumulative Hayward Brook species list, including four rare species for the region (Ireland 1982, and Schuster 1969, 1974, 1980): the moss *Plagiothecium latebricola,* and the liverworts *Lophozia bicrenata, Lophozia capitata,* and *Scapania apiculata*.

Species diversity differed among the disturbance classes at both the patch scale (â diversity) and the quadrat scale (Ædiversity). Tall and medium patches contained the greatest total number of species (57 and 55 respectively, Appendix 2) while the remaining patches ranged from 51 species on skidder trails to 45 in open patches. A consistent pattern was present in all four diversity indices (richness, evenness, Simpson=s diversity and total bryophyte cover): low remnant canopy and slash-pile quadrats had the highest and lowest values respectively, while the remaining classes were intermediate (Figure 7). Among tree height classes (tall, medium, low, open), differences between low and open quadrats were significant, while the tall and medium quadrats remained intermediate, for all diversity indices.

(2) Comparison of direct and indirect disturbance.

The first axis of the DCA clearly separated species common in areas that received direct disturbance from those that were only in areas that received minimal indirect disturbance (Figure 8). For example, *Ceratodon purpureus*, *Atrichum oerstedinum*, and *Dichodontium pellucidum* normally occur on mineral soil (Ireland 1982) and were high on DCA Axis one. *Brotherella recurvans, Bryhnia graminicolor,* and *Campylium chrysophyllum,* which are species dependent on forest substrates (tree bases, among other substrates, Ireland 1982) and *Lophocolea heterophylla* and other liverworts, which are believed to be sensitive to forestry disturbance (Söderström 1988), were low on DCA Axis one. DCA Axis 2 appeared to represent a moisture gradient. Species common in more moist to wet areas were found at central and low positions on Axis two (e.g. *Aulacomnium palustre, Polytrichum commune*), while species that are more commonly found in dry areas had high values on Axis two (e.g. *Ceratodon purpureus, Polytrichum juniperinum*).

The spread of quadrats on the first two axes of the DCA illustrated differences in both spread and central tendency of the disturbance types (Figure 9). The skidder quadrats were separated from the other disturbance types, with the highest mean value on both axes, and the greatest spread on Axis one. The substrate disturbed, open and low quadrats showed a nested pattern with their centroids (mean values on Axes one and two) in close proximity, while the spread of quadrats decreased substantially from substrate disturbed to low to open on both axes. This trend mimics the decreasing severity of indirect disturbance experienced by the community in these quadrats. The medium and tall quadrats showed a third pattern: low values on both axes, and a greater spread on Axis one than on Axis two. This emphasizes the influence of the group of species found associated with tree canopy on the spread of these quadrats (Figures 8 and 9). The trends in the bryophyte community among the disturbance classes were reflected in MRPP scores that indicate that only low and open quadrats, and tall and substrate disturbed quadrats had very similar communities. Overall, scores on both axes were positively related to the amount of direct and indirect disturbance (substrate damage and canopy removal, respectively) experienced by the quadrat. Furthermore, both DCA and MRPP results illustrate community differences between areas that had experienced catastrophic direct substrate disturbance (slash-piles and skidder trails), versus those that had experienced either relatively minor direct disturbance (substrate disturbed quadrats) or indirect disturbance.

The overlay of quadrat-level substrate and canopy variables on the DCA of species and quadrats reinforces the pervading gradient of disturbance severity in the underlying the species-quadrat pattern (Figure 10). Substrates most common in habitats that experienced direct disturbance were found high on both axes (rock, soil, and humus), while substrates most abundant in the tall tree height class, which experienced low levels of indirect disturbance, were low on both axes (trunks, needles, tall tree cover).

(3) Comparison of indirect disturbance severity

A second DCA, using only the quadrats that experienced indirect disturbance, clarified the differences among the tree height classes. Pioneer species scored high on DCA axis one (e.g. *Ceratodon purpureus*, *Polytrichum juniperinum;* Figure 11), while species common in moist to wet areas were high on Axis two (e.g. *Aulacomnium palustre, Polytrichum commune*). In the centre of the pattern, between 0 and 200 on both axes, were species that are common on rotting wood and humus (e.g. *Tetraphis pellucida, Nowellia curvifolia*). The spread of quadrats in the DCA overlapped, they illustrated differences in community among the tree height classes (Figure 12). The positions of tall quadrats were influenced by the species common on rotting wood (between 0 and 200), while the medium and low quadrats showed less spread on both axes, and their centroids were displaced upward on Axis two. The open quadrats extended higher on Axis one, as they were more influenced by pioneer species. Overall, as the amount of indirect disturbance increased (from tall to open), quadrat scores increased on both axes. Differences among the tree height classes illustrated by the DCA were reinforced by MRPP tests which indicated that community composition in tall quadrats was significantly different from that in medium, low and open quadrats (Figure 12).

An overlay of environmental variables on a DCA of species and quadrats reinforces the ranking of the tree height classes by severity of indirect disturbance (Figure 13). Rocks, roots and soil were high on both axes, while tall canopy and trunk are low on both axes. However, there were no significant correlations between percent cover of the environmental variables and quadrat scores of Axes one and two (Appendix 2).

Discussion

This study was designed to determine whether disturbance severity results in a gradient (Figure 14) in the environment and the bryophyte community, where areas that experienced the mildest disturbance contained an environment and bryophyte community little changed from pre-disturbance conditions.

Comparison of direct and indirect disturbance

Direct disturbance resulted in a greater change in the environment and the bryophyte community than indirect disturbance.

(1) Differences in the environment

The substrates, canopy and microclimate in quadrats that experienced direct disturbance differed from those that experienced indirect disturbance. For example, skidder and substrate disturbed quadrats had two to ten times higher percent cover of substrates associated with mechanical tearing and compaction of the forest floor (mineral soil, humus, rocks, roots; Table 6). In contrast, slash-pile quadrats (by definition >80% covered in slash) experienced burial of the pre-disturbance substrate during deposition of a new substrate. Direct disturbance also resulted in complete removal of the original tree canopy, and the regenerating trees four years after disturbance were predominantly <5m tall (Table 7). Consequently, the microclimate of these areas received more total PAR at a higher density (Figures 4 and 5, Table 4), and experienced mean temperatures 2-3^{0}C higher, mean VPD 8% higher, and more frequent extreme values of temperature and VPD (Figure 5 and 6, Table 4).

The open quadrats, which did not receive direct disturbance but retained no remnant canopy, represented an intermediate between substrate disturbed quadrats (Amild@ direct disturbance) and the tree height classes with remnant canopy. As a result, the substrates and canopy of the open and substrate disturbed quadrats were not significantly different (MRPP: T= 0.152, p= 0.4639). However, the microclimate in the open tree height class was moderated from that in the control area, which received direct disturbance (Figures 5 and 6, Table 4). The impact of the surrounding remnant canopy on the microclimate on a finer scale was seen in the difference in PAR between the two types of open quadrats (Figure 4).

(2) Differences in the bryophyte community

Differences between direct disturbance classes and tree height classes were also evident in the bryophyte community. As suggested in an associated study on community regeneration after harvest (Hayward Brook Watershed permanent quadrats), direct and indirect disturbance resulted in significantly different bryophyte communities (Figure 9), except for tall versus substrate disturbed. These two disturbance classes shared a core group of relatively common species, but each had a different group of infrequent species. Tall quadrats contained 11 species that were absent in the substrate disturbed quadrats (5 liverworts, 6 mosses). In contrast, pioneer species common in substrate disturbed quadrats were predominantly absent from tall quadrats (Appendix 1). It is possible that communities in the substrate disturbed quadrats were similar to those in tall quadrats before harvest, as open quadrats had the highest percent cover of stumps (Table 6) and litter composition and depth that were not significantly different from those of tall quadrats (Table 7).

Interestingly, open and substrate disturbed quadrats, whose substrates and canopy were not significantly different, contained significantly different bryophyte communities. Again, this may reflect the history of the quadrats: some open quadrats may have been naturally open areas of the pre-disturbance forest, while substrate disturbed quadrats may have been similar to tall quadrats before harvest. Alternatively, the Amild@ direct disturbance, and the potentially greater change in the microclimate due to less surrounding remnant canopy experienced by substrate disturbed quadrats, may have been enough to cause a greater change in the bryophyte community.

The differences between bryophyte communities that received direct vs indirect disturbance was illustrated by the occurrence and frequency of liverworts, which are considered particularly vulnerable to forestry disturbance (Söderström 1988), and pioneer species, which are infrequent in undisturbed forests (Sims 1996, Jonsson and Esseen 1998, Rydgren et al. 1998). For example, the frequencies among disturbance classes of *Lophocolea heterophylla*, and *Ceratodon purpureus,* a ubiquitous liverwort and pioneer moss, respectively (Crum 1976, Schuster 1980), were inversely correlated (Table 9). *L. heterophylla*, commonly occurs on moist rotting wood, but also occupies many different habitats, including Ahighly disturbed woodlands and along fence rows@ (Schuster 1980). Despite being a relatively abundant and robust liverwort, it clearly declined in frequency with increasing disturbance, from indirect (tall to open) to direct (substrate disturbed to slashpile; Table 9 and Appendix 1). *C. purpureus*, a typical pioneer species (sensu During 1992) with a relatively high reproductive output of small spores (11-15Φm, Crum 1976), tends to appear in a community early in succession (Crum 1976). *C. purpureus* occurred in 20% of quadrats on skidder trails, but occurred in only 0-6% of quadrats under remnant canopy (Table 9), and in the Hayward Brook pre-harvest forest (Sims 1996 and Fenton 2001).

Impact of indirect disturbance severity

This study addressed a second issue: whether there was a gradient of disturbance severity within the tree height classes (Figure 14). Patches that had the most canopy removed would have experienced the most severe microclimatic disturbance. Because bryophytes are sensitive to microclimatic change, these areas would also have experienced the greatest change in the bryophyte community characteristics, including, species diversity, total bryophyte abundance, species frequency, and abundance. A more scientifically rigorous method to test the proposed gradient would be a Abefore and after@ sampling design, however this was not feasible. By examining habitats (microclimate and substrates), bryophyte community and species characteristics, as well as considering the potentially confounding effect of the pre-harvest community, it is possible to establish the presence of the gradient.

(1) Environment

In order to determine whether the proposed gradient of indirect disturbance severity has influenced the bryophyte community under remnant canopy, it is first necessary to demonstrate that the tree height classes had different tree structures, which resulted in different microclimates. Equally important is discounting differences in naturally available substrates as a driving environmental factor in the bryophyte pattern.

Remnant canopy patch structure (tree height, tree density, and basal area and the proportion of *Abies balsamea*) varied with the proposed indirect disturbance severity gradient (Table 3). This created a gradient in the amount of tree cover available to the bryophyte community. The larger size of the tall patches may have resulted in a higher interior edge ratio, and provided larger patches of effective habitat (Saunders et al. 1991). This may have confounded the structural differences of the tall patches.

Differences in remnant canopy patch structure were reflected in a gradient in microclimatic conditions. Means and ranges of temperature and VPD increased with decreasing remnant canopy (Table 4, Figures 5 and 6). However, tall patches had higher means of total daily PAR and incident PAR density. This may be a reflection of the mixed tree composition of these patches. In early spring before the deciduous trees budded, incident PAR in the tall patches was higher than during any other point of the sampling period and increased the mean incident PAR density (Figure 3). Rambo and Muir (1998) used basal area as a surrogate variable for available PAR, however basal area and available light were not correlated in this study, as the tall patches with the highest basal area had intermediate values of available PAR. This discrepancy may be due to stand age; Rambo and Muir (1998) were comparing mature forests whereas the remnant canopy at Hayward Brook is mostly juvenille trees which have not experienced self-thinning. The low basal area of low and medium patches may not be an accurate reflection of tree density, and the amount of light reaching the forest floor. Further, the deciduous component of tall patches, which resulted in a higher frequency of bright light reaching the forest floor, was not present in the *Pseudotsuga menziesii-Tsuga heterophylla* studied by Rambo and Muir (1998).

Percent cover of available substrates did not follow the pattern predicted by the indirect disturbance gradient (Table 6). The exception is percent cover of needles, which decreased with increasing disturbance severity. This would be expected as needle litter is a reflection of the canopy above as well as an available substrate for bryophytes. If the bryophyte community followed the indirect disturbance gradient, patch structure and microclimate played a greater role in structuring the community than available substrates.

(2) Bryophyte community

The forest floor bryophyte community followed the indirect disturbance gradient imperfectly, because the bryophyte community that was present in 1999 was a product of both the disturbance severity experienced, and the composition and diversity of the pre-disturbance community.

The response of the bryophyte community to disturbance severity is visible in community and species characteristics. The quadrat scores on the first two DCA axes were positively correlated with severity of indirect disturbance experienced by the quadrat (Figure 12).

At the species level, we would predict that forest floor species would be more common in tall patches than in low or open patches. However, this was moderated by the individual microclimatic tolerance ranges of species as plants responded on different levels, from impaired reproduction to death (Lichtenthaler 1996). Liverworts (e.g. *Lophocolea heterophylla*), which have been found to be most affected by forest management (Gustafsson and Hallingbäck 1988, Lesica et al. 1990, Ross 1999), were particularly sensitive to variations in remnant canopy levels and were more abundant in tall than in low or open patches. In contrast, other species (14 mosses and 11 liverworts) showed no response to different amounts of remnant canopy, but rather to the presence of any remnant canopy. For example, the frequency of *Brachythecium reflexum* and *Callicladium haldanianum* dropped from 8 and 11 in low quadrats to 4 and 5 in open quadrats (Appendix 1).

The ameliorative effect of a small amount of shade on the bryophyte community has been sporadically reported in the literature. Busby et al. (1978) documented a slower growth rate *Hylocomnium splendens* after removal of shrub and herb layers which resulted in completion of growth one month later than in undisturbed sites, while Olsson and Staaf (1995) and Peterson (1999) commented on a higher percent cover of bryophytes under slash cover. Beese and Bryant (1999) monitored bryophyte communities before and after harvest by a variety of methods including clearcuts and shelterwood cuts (where seed trees are left on site to provide seeds and to reduce the microclimatic change experienced by the forest floor; Nyland 1996). Three years after harvest, bryophyte communities beneath shelterwood cuts were not significantly different from pre-harvest communities, and had maintained half of their original percent cover. All of these results indicate that bryophytes not only respond to microclimatic gradients created by varying levels of forest cover, but that even low canopy cover provided by either slash or advanced regeneration provides some protection from indirect disturbance.

While the bryophyte community pattern varied along the indirect disturbance gradient, it was also influenced by the pre-disturbance community, as quadrats that contained potentially sensitive forest floor species and that had high initial diversity were more likely retain these characteristics after harvest. For example, species such as the liverwort *Cephalozia bicuspidata*, which are most frequent in medium and low quadrats (Appendix 1), are more likely to reflect their pre-disturbance distribution then the disturbance gradient. Furthermore, because bryophyte community diversity and abundance may be influenced by bryophyte hydration time (Tamm 1950, Økland et al. 1999), and habitat diversity (Jonsson and Essen 1990), characteristics of the pre-harvest canopy retained as remnants likely affect the potential initial community composition. For example, the low diversity and total bryophyte cover of the tall quadrats (Figure 8) may be the legacy of the dense sapling canopy, which intercepts precipitation and limits incident precipitation reaching the forest floor (Table 4), bryophyte hydration time and ultimately bryophyte growth (Tamm 1950, Päivänen 1966 and Hansen et al. 1993).

The higher values of richness (9 species per quadrat compared to 7), and diversity (0.6 compared to 0.5) in low and medium patches may also be legacies of the previous canopy. These remnant canopy patches, dominated by *Abies balsamea*, may have been sites of relatively recent tip-ups, which are an important factor in the disturbance regime of the Acadian forest (Woodley and Forbes 1997), and provide a favourable environment for *Abies balsamea* advanced regeneration (Kneeshaw and Bergeron 1998). Tip-ups and resultant forest gaps provide a diverse environment for bryophyte communities (Jonsson and Esseen 1990), and allow more rain to reach the forest floor. The potential of a more diverse habitat in the past, increased precipitation and bryophyte hydration time, along with the intermediate level of indirect disturbance experienced after harvest, may explain the high diversity and bryophyte cover found in these remnant patches (Figure 8).

Conclusions

Patches of remnant canopy, as are currently left in clearcuts in areas with abundant advanced regeneration, represent refugia for forest floor bryophyte species. The environmental conditions created by indirect disturbance were sufficiently similar to pre-harvest conditions to allow many forest floor bryophyte species to survive. Furthermore, an indirect disturbance severity gradient was created among remnant canopy classes, illustrated by the positive correlation between the amount of canopy removed and forest floor microclimatic conditions. The pattern of the post-disturbance bryophyte community varied along the gradient of indirect disturbance severity and reflected the pre-disturbance community.

Remnant canopy patches may promote the conservation of bryophyte diversity within a managed forest landscape by increasing the survival of established populations, thereby reducing the dispersal distance from source populations, and perhaps recolonization time of harvested areas. However, further research is needed to determine: (1) whether refugia size and shape influence bryophyte survival, (2) whether bryophyte populations within refugia contribute to the re-assembling bryophyte community, and (3) the degree to which the results of this study are the consequence of the distribution of the pre-disturbance bryophyte community.

Part 2: Riparian buffers as refugia

Introduction

Globally, riparian zones (land immediately adjacent to watercourses) contain diverse vegetation (Nilsson et al. 1993), and play a role in water quality preservation (Correl 1996), however $\geq$ 80% of riparian zones in North America and Europe have disappeared in the last 200 years (Naiman et al. 1993). Although this decline has sparked interest in their conservation, multiple definitions of riparian zones impede conservation. Biologically, riparian zones include (a) the area between high and low water levels, or (b) the areas from low water, upland to where plants are no longer affected by high water tables, periodic flooding, and moist soils (Naiman and Décamps 1997). Their definition is further confused by the forestry industry defining riparian buffers as strips of forest of generally uniform width (e.g. 60m), left (somewhat) intact along watercourses. These strips are assumed to encompass the riparian zone and its functions, as well as to preserve plant and animal habitat and to provide corridors for movement across the landscape. It is important to assess whether riparian buffers accomplish the conservation goals for which they are intended.

Vegetation in the riparian zone

Riparian zones are some of the most diverse and dynamic areas in temperate and boreal forests (Nilsson et al. 1993). For example, 13% (>260 species) of Sweden=s vascular plant flora was found along one river corridor (Nilsson 1992), including upland species that may be rare components of the riparian flora (Naiman et al. 1993). Unlike upland forests beyond riparian zones, which are structured by gap or stand replacing disturbance regimes, riparian zone vegetation is structured by the processes associated with water flow, water level fluctuation, and sediment and litter transport (Nilsson et al. 1993). Frequent, patchy disturbances create a diverse environment with a plant community composed of species capable of either surviving erosion and deposition of sediments and litter, or dispersing into the altered habitat. Although erosion and deposition become less important with increasing height above high water, the vegetation may be influenced by high humidity, high water tables, and rare flooding events (Naiman and Décamps 1997), hence the vegetation varies along a gradient from stream to upland forest.

Potential roles of riparian buffers in conservation

In New Brunswick, regulations require that a forested buffer $\geq$ 30m be left on either side of a waterway (DNRE 1996). This buffer strip encompasses the riparian zone vegetation, which preserves stream water quality by removing suspended particles, dissolved nutrients, toxins, and pesticides from overland storm water (Correl 1996). Vegetation in the riparian zone also shades the stream and provides coarse woody debris, which maintains fish, amphibian and invertebrate populations (Woodley and Forbes 1997). Furthermore, because riparian buffers create corridors across an increasingly fragmented landscape, they are frequently regarded as potential corridors for plant and animal migration (Gregory et al. 1991, Spackman and Hughes 1995, Woodley and Forbes 1997) and refugia from disturbance in the upland forest (Naiman and Décamps 1997). However, few studies have tested the effectiveness of riparian buffers as either corridors or refugia for plants, particularly for bryophytes.

The goals of this study are to determine whether the riparian buffer in Hayward Brook:

(1) includes sufficient members of the pre-harvest upland forest floor bryophyte community to act as a refugium for the re-assembling forest floor community in clearcuts,

(2) includes those species which have been identified as being at risk of local extirpation as a result of forest harvest in permanent quadrat studies (Fenton 2001, Peterson 1999). This study cannot address whether in 1995 the riparian buffer contained members of the pre-harvest community, or particularly those species identified at risk.

(3) contains species that were found in the upland forest only after harvest. If it does, this study will not be able to determine whether the riparian buffer is contributing propagules to the post-harvest community, both communities are being structured by similar disturbance patterns, or both communities are receiving the same air-borne propagules as colonists.

Methods

Study site

This study took place in the Acadian mixed forest region sites described in Part 1. The forest managers designated 60m on each side of the Hayward Brook as a riparian buffer, and applied various harvest operations to the adjacent upland stands as described in Peterson (1999), and Frego (1998).

Quadrat establishment and sampling

Thirty-six plots were established in the riparian buffer at 25 metre intervals approximately midway between the stream and the edge of the adjacent cut block. In summer 2000, environmental features and bryophyte data were recorded for one 1.25 m^2 quadrat per plot (the same plots were used in a related study by Dr. M. Roberts, Forestry, UNB). Height above (m) and distance from (m) the persistent stream course were also recorded. Bryophyte abundance (% cover by species) and substrate were recorded; voucher samples of bryophytes were collected for identification in the laboratory and remain in the herbarium at the University of New Brunswick, Saint John. Taxonomy follows Ireland (1982) and Crum and Anderson (1981) for the mosses and Schuster (1969, 1974,1980) and Ireland and Bellilio-Trucco (1987) for the liverworts.

Upland forest vegetation was represented by data from permanent quadrats in the adjacent upland clearcuts, collected in 1995 (pre-harvest) and 1999 (post-harvest). Fourteen permanent quadrats classified as Abuffer@ were included as part of the buffer system in analyses. Sampling methods were the same as for the buffer quadrats.

Statistical analysis

The riparian buffer bryophyte data set from 2000 was compared to those from 1995 (pre-harvest) and 1999 (post-harvest) permanent quadrat data sets. To test whether the communities in question were significantly different overall, multi-response permutation procedure (MRPP; McCune and Mefford 1999) and similarity indices were calculated. Two detrended correspondence analyses (DCA; ter Braak and Šmilauer 1998) were used to summarize the multivariate pattern of the riparian buffer community, and 1995 (buffer/pre-harvest) and 1999 (buffer/post-harvest) upland communities respectively. Quadrats containing less than five species were passively placed into the pattern, as recommended by Økland (1990). Diversity indices (richness, evenness and Simpson=s diversity index) were calculated for the three data sets. Total % bryophyte cover, a measure of bryophyte abundance calculated as the sum of individual species, was log-transformed (total % cover +1) to reduce heterogeneity of variances. Homogeneity of variances of diversity indices and transformed total bryophyte cover was tested using Levene=s statistic. If differences in variances were significant, the Mann-U Whitney test was used, otherwise t-tests were used. Diversity indices, and the scores on the first two DCA axes (buffer/pre-harvest) of the buffer quadrats were tested for correlation (Spearman=s rho) with height above, and distance from the stream and distance from the edge of the buffer. One quadrat (B-13) was identified as an outlier and deleted from the correlation analyses; it was the only quadrat located in an ephemeral stream bed.

Results

Does the riparian buffer act as a refugium?

The bryophyte community in the riparian buffer at Hayward Brook was very rich; 71 species were found in 32 m^2 , compared to 88 species in 159 m^2 in the pre-harvest upland forest (Fenton 2001). The riparian buffer included 56 of the 82 (68%) species found in the pre-harvest upland community. However, of the nine bryophyte species Alost@ from the permanent quadrats after harvest, only two were found in the riparian buffer: epiphytes *Frullania oaksiana* and *Ulota coarcata* (Ireland 1982, Ireland and

Bellilio-Trucco 1987; Table 1).

Although the riparian buffer and pre-harvest communities shared 56 species (57.7% similarity, Table 2), they were significantly different overall (Table 2). The first DCA axis illustrates some of these differences: riparian buffer quadrats ranged higher on the first DCA axis than did pre-harvest quadrats (Figure 1). While total bryophyte cover was not significantly different (Figure 2A), other diversity indices differed between pre-harvest and riparian buffer communities: riparian buffer quadrats were richer, more even, and more diverse than pre-harvest quadrats. The higher evenness of riparian buffer quadrats (0.73 versus 0.59) is due to the reduction in percent cover when present of large dominant speices of the pre-harvest community such as *Pleurozium schreberi, Dicranum polysetum, Dicranum scoparium,* and *Hylocomnium splendens.* For example, the mean percent cover when present of *P. schreberi* dropped from 6.83% in pre-harvest quadrats to 0.77% in the riparian buffer quadrats.

Height above the stream was weakly correlated (r=-0.386) with buffer quadrat scores on the first axis of the pre-harvest/buffer DCA and with richness (Table 3). Richness was also correlated with distance from the stream (Table 3).

Could the riparian buffer act as a source of species to the upland forest post-harvest?

The riparian buffer contained 15 species that were not present in the pre-harvest community (Table 1). Two of these species, *Ulota coarctata* and *Dicranum fulvum*, were found in the post-harvest community (Fenton 2001). Although the riparian buffer and post-harvest (1999) bryophyte communities had similar community compositions (55%; Table 2), they were still significantly different (MRPP; Table 2).

While the post-harvest community was significantly different from the riparian buffer community, it was less different than was the pre-harvest community. The MRPP T-value (which expresses Euclidean distance between groups) comparing the post-harvest and buffer communities was lower than that comparing pre-harvest and buffer communities, and Figure 3 illustrated a greater overlap of bryophyte communities in riparian buffer and post-harvest quadrats. Furthermore, evenness of buffer quadrats were not greater than the post-harvest quadrats (Figure 2B). Like the buffer, quadrats in the post-harvest community that had experienced direst disturbance were not dominated by large patches of *Pleurozium schreberi, Dicranum polysetum, Dicranum scoparium,* and *Hylocomnium splendens* (Fenton 2001).

The riparian buffer quadrat B-13, which was in an ephemeral stream bed, was unusually rich (27 species). It contained five species unique to that quadrat and one species found only in the buffer (Table 1). Its intermediate score on the first DCA axis (buffer/pre-harvest) is somewhat misleading, as it reflects the passive insertion of the quadrat based on scores for its non-unique species. Even so, it had the highest first axis score in the buffer/post-harvest DCA (Figure 3), where it was positioned with post-harvest quadrats that had received particularly severe substrate compression and were therefore very wet (pers. obs.).

Discussion

The results of this study illustrate three points: (1) the high floristic diversity of the riparian zone, (2) the dissimilarity of the riparian buffer and the upland pre-harvest communities, and (3) the potential convergence of riparian buffer quadrats and upland quadrats that received direct disturbance.

Riparian buffer: potential bryophyte refugium

The riparian buffer zone in Hayward Brook applied by forestry managers did not act as an effective refugium for forest floor bryophyte species. It did not contain the eight species that were documented as being at risk of local extirpation after harvest of adjacent forest stands (Fenton 2001, Peterson 1999).

However, the riparian buffer illustrated the typical riparian vegetation pattern of high richness and evenness (Naiman and Décamps 1997) and increasing similarity of riparian buffer to upland pre-harvest community with increasing height above the stream (Figure 1 and Table 3). Quadrat B-13 underscores both these points. The high richness of quadrat B-13 reflects the impacts of intermittent water flow, sediment and litter deposition, and moist soils on riparian buffer vegetation. Furthermore, the high richness of this quadrat (27 species) was not so much an outlier as the extreme end of a gradient that was only partially sampled in this study, i.e. if a transect was established from the upland forest to the edge of the stream, quadrat B-13 would be one end point. Jonsson (1997) found similar trends of decreasing bryophyte richness with height above the stream in the Cascade Mountains.

Although the riparian buffer did not act as refugium for forest floor species, similarity between the riparian buffer and upland forest communities was correlated with height above the stream. If the mean height above the stream required to capture sufficient members of the upland forest community was determined and established as the outer limit of the riparian buffer maintained during harvest, the buffer would have increased potential to act as a refugium.

Riparian buffer: source of invading species in upland forest post-harvest

This study has provided no evidence that the riparian buffer acted as a source of propagules for new species to invade the re-assembling upland community four years after forest harvest. The two species that were present in the riparian buffer zone and in post-harvest communities were not species that commonly invade disturbed habitats. *Ulota coarcata* is an epiphyte that usually grows on deciduous tree trunks in moist forests (Crum and Anderson 1981). The presence of this species in post-harvest communities is not surprising, as colonies may have been attached to deposited slash. *Dicranum fulvum* grows in deciduous woods on shaded acid rocks (Crum and Anderson 1981), and was infrequent in both the riparian buffer zone and post-harvest communities (one and two occurrences, respectively; Table 1 and Fenton 2001). Its presence in both communities is unlikely to represent colonization from the riparian buffer zone to the post-harvest community; it is more likely to be attributable to colonization of both areas from a source population.

However, communities in the riparian buffer quadrats and those that received direct disturbance may be converging. Quadrat B-13 and several wet upland quadrats that received particularly severe substrate compression (pers. obs.) had high scores on the first axis of the buffer/post-harvest DCA (Figure 3). The species in B-13 and these quadrats characteristically colonize mineral soil and grow in wet conditions. The severe disturbance experienced by the upland quadrats created a habitat similar to that of an ephemeral stream bed (B-13). The similarity of the communities in these quadrats is not an invasion from the riparian buffer, but rather the consequence of habitat convergence.

Conclusions

In spite of high floristic diversity, the 60m riparian buffer along Hayward Brook does not act as a refuge for upland forest floor bryophyte species because it contains a significantly different bryophyte community. Specifically, it lacks the eight species determined to be at risk in the adjacent upland forest community. However, similarity between the riparian buffer and upland forest communities is correlated (r= -0.386) with height above the stream. These results suggest that if the mean height above the stream required to capture sufficient members of the upland forest was determined and established as the outer limit of the riparian buffer maintained during harvest, the riparian buffer would have increased potential to act as a refugium.

The riparian buffer is also not acting as a source of new species in the re-assembling upland community. The convergence of the riparian buffer zone community and that found in quadrats that experienced direct disturbance may not extend beyond canopy closure, or may result in a different forest floor community. Regardless, the convergence is more likely the result of habitat restrictions on the applicant species of community re-assembly. This requires further study.

Riparian buffers are rich and ecologically important components of our landscape. This study determined that six bryophyte species were found only in the riparian buffer zone (e.g. quadrat B-13) and not in the adjacent upland forest that is subject to harvest. Study of adjacent upland forests indicates that disturbance of the forest floor results in the greatest loss of species (Part 1, Fenton 2001), therefore any harvesting activities that would damage the forest floor in the riparian buffer will put its species at risk of local extirpation. Species commonly found in the riparian buffer may be even more susceptible to disturbance than typical upland species because they occupy a small fraction of the landscape, and may have narrower microclimatic and substrate requirements than most forest floor bryophyte species. Therefore these direct and indirect disturbance should be minimized within riparian buffers.

Part 3. General discussion: Potential refugia for forest floor bryophytes

In order for an area to be an effective refugium, it must meet two criteria: (1) provide appropriate habitat (microclimate and substrates) for sensitive forest floor species, and (2) contain these species. Given the limits on bryophyte dispersal, it is unreasonable to expect that presence of habitat is equivalent to presence of species. Further, Odum (1985) and Rapport et al. (1985) argue that a refugium should show few characteristics of a stressed community, (a) increased proportion of r-strategists, (b) decreased life span of organisms (or parts), (c) decreased size of organisms, (d) decreased species diversity, and increased dominance, in communities where initial diversity was high, but increased diversity if original community diversity was low.

(1) Remnant canopy

The habitat and the bryophyte community of indirectly disturbed areas in the clearcut were clearly different from areas that experienced direct disturbance (Part 1 and Fenton 2001), and were shown to act as refugia for forest floor bryophyte species. However, the classes of indirect disturbance, characterized by height of their remnant canopy, were not equally effective as refugia. Patches of remnant canopy of low and medium height were the most effective refugia, because they provided a habitat similar to pre-disturbance conditions, and contained the species sensitive to forest harvest. The tall remnant canopy, which experienced the least severe disturbance, was the least effective refugium because it contained fewer sensitive species.

Evidence of Odum=s characteristics of stressed systems was more prevalent in open and low than in medium and tall tree height classes. While the dichotomy of K- vs r-strategies is not usually applied to bryophytes (cf. Slack 1977), many characteristics of r-strategists are incorporated in life-strategy systems intended for bryophytes. For example pioneers, described by During (1992) as having numerous light spores and a short life span, were more frequent in the open and low quadrats than in the medium and tall quadrats. Many of these pioneer species not only had a higher reproductive output and a shorter life span than dominant forest floor bryophytes, but were also smaller in size. Further, diversity was lowest in the open tree height class and highest in the low tree height class. High diversity in this class may be a relict of the pre-disturbance forest, however it may also be a result of the diverse habitat created by disturbance.

Of the tree height classes, medium height remnant canopy appears to be the most effective refugium, as it contains the species most at risk, provides the appropriate habitat and has few characteristics of a stressed community. It should be noted that this is not the tree height class which experienced the least disturbance, nor is it the most diverse.

(2) Riparian buffer

The riparian buffer was not an effective refugium. It did not contain the species that were most sensitive to forest harvest, although it contained appropriate substrates, a humid microclimate by definition, and experienced no anthropogenic disturbance. The current designation of the riparian buffer of uniform width >30m provides effective protection of water quality (Correl 1996). However, if the boundary of the riparian buffer was extended to a height above the stream that captured sufficient members of the upland community to act as a propagule sources, it may be able to act as a refugium. If plans to selectively harvest riparian buffers are implemented, potential refugium qualities may be lost, and an additional bryophyte community would be put at risk: those restricted to the riparian zone.

Recommendations

Recommendation 1

Remnant canopy protects forest floor bryophytes from microclimatic changes caused by canopy removal. Patches of remnant canopy greater than 1.5 metres tall provided the best protection from microclimatic change, and contained the most species considered to be potentially at risk.

(A) Patches of advanced regeneration >1.5m tall should be left within clearcuts to act as refugia for bryophytes sensitive to forest harvest.

(B) Research should be undertaken to determine the optimum size, shape and spatial distribution of refugia to allow preservation of populations.

While this study was not undertaken to test the effect of patch size, on refugia quality, at a minimum patches should not be smaller than $14.6m^2$, the mean medium patch size. Patch shape should minimize edges, and be distributed to minimize dispersal distance.

Recommendation 2

Riparian buffers of equal width, as currently maintained by the forestry industry (to 60m at Hayward Brook), are not as effective as refugia for the bryophyte community of the adjacent upland forests because they do not contain the same bryophyte community. However, if riparian buffers are to act as refugia for upland forest floor bryophytes,

(A) the width of riparian buffers should be increased to a height above the stream which includes the upland pre-harvest community.

Furthermore, because many bryophyte species are restricted to the riparian buffer, and because they are more likely to be sensitive to microclimatic change than upland species,

(B) harvesting within the riparian buffer should be undertaken with extreme caution as it puts these species at risk of local extirpation.

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Part 1 Tables:

Table 1: Characteristics of transects. Elevation and distances measured using GIS data.

Transect	Length (m)	Elevation (m)	Distance from road (m)	Distance from stream (m)
1	14	71	57	61
2	13	67	191	45
3	20	75	198	153
4	17.5	71	292	66
5	17	87	40	286
6	16	76	124	97
7	17	76	60	120
8	16	77	14	160
9	17.5	83	37	208
10	14	86	45	263
11	19.5	69	177	84

Table 2 : Available substrates (forest floor not colonized by bryophytes) measured within 0.5 x 0.5m quadrats.

Substrate	Description	Substrate	Description
mineral soil	exposed mineral sub-soil layer	**scat**	animal droppings
humus	fine texture, well decomposed organic matter	**twigs**	coniferous or deciduous woody material with diameter < 1 cm
stumps	bases of cut trees	**fine woody debris**	coniferous or deciduous woody material with diameter >1 cm and < 5 cm
roots	exposed woody tree roots	**coarse woody debris**	coniferous or deciduous woody material with diameter > 5 cm
rocks	exposed consolidated minerals	**bark**	pieces of loose coniferous or deciduous bark
trunks	cross section area of living woody plants in the quadrat	**leaves**	unattached dead deciduous leaves
needles	loose conifer needles	**cones**	pine and spruce cones

Table 3: Patch level characteristics by tree height class: tall trees >5m in height, medium 1.5-5m in height, low <1.5m in height, open no remnant canopy. Values are means ± standard error; means followed by the same letter within a row are not significantly different. Letters also indicate ranking (i.e. a < b < c).

	Tall	Medium	Low	Open
# of patches	7	8	6	9
# of quadrats	71	57	43	62
mean area (m^2)	37.494 b ± 8.47	14.603 a ± 2.56	10.20 a ± 3.95	9.01 a ± 1.35
mean tree height (cm)	475.99 c ± 19.70	195.96 b ± 6.51	119.81 a ± 3.06	NA
tree density (trees m^{-2})	1.687 a ± 0.295	2.661 a ± 0.646	3.79 a ± 1.42	NA
basal area (cm^2m^{-2})	42.920 a ± 4.05	30.928 b ± 2.36	8.450 c ± 1.62	NA
dominant tree species (frequency)	*Picea* spp. (42%) *Abies balsamea* (45%)	*Abies balsamea* (66%)	*Abies balsamea* (75%)	NA

Table 4: Microclimatic variables for tree height classes from April 25 to September 26, 2000. Tall trees >5m in height, medium 1.5-5m in height, low <1.5m in height, open no remnant canopy, control in clearcut. Total precipitation in ml, PAR density in ìms^{-1}m^{-2}, temperature in ^{0}Celsius, and VPD as %. (Minimum PAR density = 0 for all classes.)

Variable		Tall	Medium	Low	Open	Control
Precipitation	total precipitation	2021.2	6112.8	3153.6	3621.2	3456.4
	mean precipitation/ sampling period[1]	135.2	203.7	210.2	241.7	265.7
	standard error	34.3	51.9	55.5	50.9	60.2
PAR density	mean	19.52	16.20	18.30	171.76	403.87
	max	338.40	564.6	750	1825.0	2063
Temperature	mean	14.56	14.80	14.85	15.77	17.46
	min	-3.61	-3.90	-4.01	-5.89	-5.84
	max	35.20	34.46	33.05	44.04	45.96
VPD	mean	8.21	12.10	11.62	11.93	17.58
	min	0	0	0.04	0	2.52
	max	40.09	42.85	35.28	66.58	95.98

[1] Sampling periods varied from 1-3 weeks.

Table 5: Differences among disturbance types in substrates (upper right triangle) and herbaceous canopy (lower left triangle). Values are multi-response permutation procedure (MRPP) test statistic T followed by the probability of obtaining that value of T by chance alone. Bold values are **not** significant at the Æ= 0.05 level.

	Tall	Medium	Low	Open	Substrate disturbed	Skidder	Slash-pile
Tall		- 2.36 0.04	-11.22 <0.01	-19.37 <0.01	-18.01 <0.01	-22.27 <0.01	-24.83 <0.01
Medium	-3.55 <0.01		-3.35 0.02	-10.73 <0.01	-10.17 <0.01	-15.78 <0.01	-19.66 <0.01
Low	-4.82 <0.01	**0.33** **0.486**		-5.40 <0.01	-5.84 <0.01	-11.91 <0.01	-16.27 <0.01
Open	-12.35 <0.01	-2.72 <0.01	**-0.74** **0.16**		**0.98** **0.4**	-11.11 <0.01	-11.11 <0.01
Substrate disturbed	-35.69 <0.01	-41.16 <0.01	-35.08 <0.01	**-1.10** **0.12**		**-1.71** **0.06**	-8.98 <0.01
Skidder	-40.82 <0.01	-44.00 <0.01	-46.7 <0.01	-10.28 <0.01	-12.74 <0.01		-12.67 <0.01
Slash-pile	-19.01 <0.01	-23.31 <0.01	-23.93 <0.01	-7.05 <0.01	-3.87 0.02	-12.56 <0.01	

Table 6: Percent cover of substrates grouped by disturbance class. Values are means + standard errors; means followed by the same letter in a row are not significantly different at the p<0.05 level. Letters also indicate ranking (ie: a < b < c < d).

	Tree height classes				Direct disturbance classes		
	Tall	Medium	Low	Open	Substrate disturbed	Skidder	Slash-pile
rocks	0.24 ab + 0.22	0.009 a + 0.009	0.07 ab + 0.052	0.20 ab + 0.103	0.04 ab + 0.039	1.02 b + 0.40	0.0 a + 0.0
trunks	1.64 b + 0.30	0.98 ab + 0.183	0.90 ab + 0.352	0.41 a + 0.241	0.49 a + 0.141	0.23 a + 0.16	0.15 a + 0.11
stumps	0.21 a + 0.21	1.20 a + 0.90	0.00 a + 0.00	0.12 a + 0.16	3.70 a + 1.97	0.91 a + 0.47	0.0 a + 0.0
mineral soil	0.018 a + 0.015	0.18 a + 0.18	0.12 a + 0.095	0.21 a + 0.14	0.43 a + 0.26	1.97 b + 0.50	0.11 a + 0.11
humus	0.70 a + 0.31	0.67 a + 0.24	0.72 a + 0.30	1.15 ab + 0.47	3.89 b +1.56	1.90 ab + 0.51	0.11 a + 0.11
bark	2.36 ab + 1.03	1.93 ab + 0.688	2.92 ab + 0.742	1.49 a + 0.316	3.54 ab + 0.822	2.16 a + 0.39	5.13 a + 1.82
cones	0.39 ab + 0.098	0.12 a + 0.043	0.86 b + 0.294	0.15 a + 0.053	0.25 a +/- 0.132	0.26 a + 0.11	0.11 a + 0.076
scats	0.63 bc + 0.10	0.64 bc + 0.104	0.68 c + 0.101	0.63 bc + 0.088	0.22 ab + 0.038	0.37abc + 0.10	0.11 a + 0.058
needles	52.56 d +3.92	45.56 cd + 4.40	32.25 bc + 4.64	21.56 ab + 3.69	20.55 ab + 2.90	14.66ab +2.76	7.14 a + 1.82
leaves	25.86ab + 2.40	18.85 a + 2.60	14.13 a + 1.69	28.53 ab + 3.36	25.02 ab + 3.66	36.41 b +4.11	15.86 a + 2.85
roots	0.42 a + 0.139	0.73 a + 0.438	0.99 a + 0.495	0.78 a + 0.429	1.57 a + 0.644	2.43 a + 0.78	1.22 a + 1.11
twigs	7.23 a + 0.833	11.44 a + 1.82	11.25 a + 1.25	11.81 a + 1.66	11.78 a + 1.78	8.09 a +1.28	30.44 b +-5.32
woody debris	10.71 a + 2.23	14.59 ab + 2.00	17.20 ab + 2.23	24.37 b + 2.68	26.46 b + 1.78	18.68ab + 1.28	43.22 c + 5.31
substrate richness	6.46 b +0.159	6.33 ab +0.194	6.74 b + 0.251	6.03 ab + 0.263	6.29 ab + 0.257	6.00 ab + 0.33	5.17 a + 0.373

Table 7: Litter characteristics grouped by disturbance class. Litter ratio scale: 100% needles = 0.1; 100% leaves = 1.1. All values are mean ± standard error. All litter values are means of four sub-samples per quadrat. Means followed by the same letter in the same row are not significantly different at the $p<0.05$ level. Letters also indicate ranking (i.e. a< b< c <d).

	Tree height classes				Direct disturbance classes		
	Tall	Medium	Low	Open	Substrate disturbed	Skidder	Slash-pile
needles: leaves ratio	0.32 ab ± 0.035	0.25 a ± 0.038	0.23 a ± 0.036	0.43 ab ± 0.053	0.39 ab ± 0.051	0.55 b ± 0.064	0.45 ab ± 0.126
litter depth (mm)	13.56 c ± 0.833	12.49 bc ± 1.09	9.08 b ± 0.829	8.10 b ± 0.838	9.49 bc ± 1.03	8.65 b ± 1.02	2.96 a ± 1.19

Table 8: Percent cover quadrat level canopy by disturbance class. Mean rank (low PAR = low rank) by disturbance class of means of four sub-sample values of PAR is also shown. Total herbaceous calculated as the sum of individual species cover values. Values are means ± standard error; means followed by the same letter within a row are not significantly different. Letters also indicate ranking (i.e. a < b < c < d).

	Tree height classes				Direct disturbance classes		
	Tall	Medium	Low	Open	Substrate disturbed	Skidder	Slash-pile
total tree	57.16 b ±4.01	63.12 b ±3.80	62.21 b ±4.37	16.35 a ±2.39	18.75 a ±2.60	11.34 a ±2.27	9.39 a ±2.45
high	44.57 b ±3.95	0.61 a ± 0.40	0.23 a ± 0.23	3.73 a ±1.81	1.08 a ± 0.70	0.82 a ± 0.67	0.0 a ± 0.0
medium	6.50 a ±1.89	56.11 b ±3.97	2.67 a ±2.11	4.40 a ± 1.24	7.12 a ±1.46	7.21 a ±2.10	6.11 a ±2.44
low	6.086 a ±1.49	6.404 a ±1.92	59.30 b ±4.36	8.226 a ±1.73	10.55 a ±2.61	3.28 a ± 1.08	3.37 a ± 1.48
total herbaceous	9.80 ab ±1.83	15.22ab ±2.29	18.10ab ±3.14	22.61 b ±2.56	17.91ab ±2.94	37.67 c ±3.62	6.85 a ± 2.09
Vaccinium spp.	1.40 a ± 0.46	0.92 a ± 0.28	2.09 a ± 0.67	3.24 a ± 0.67	3.32 a ± 0.80	2.87 a ± 0.98	1.14 a ± 0.86
Cornus canadensis	1.196 a ± 0.418	5.25 ab ± 1.20	5.07 ab ± 1.09	6.86 b ±1.628	4.35 ab ± 1.253	2.68 ab ± 0.856	0.014 a ±0.014
Pteridium aquilium	1.50 ab ± 0.43	0.75 a ± 0.37	0.12 a ± 0.12	2.79 ab ± 0.77	2.31 ab ± 0.672	4.34 b ± 1.10	2.33 ab ±1.08
PAR rank	76.10 a ±10.28	95.64 ab ±9.67	128.03 bc ± 10.87	170.03 cd ±10.61	216.87 d ± 10.38	203.45d ±9.47	204.76d ±17.91

Table 9: Frequency of occurrence of contrasting ecology by disturbance class. Values are % of quadrats.

species	Tall	Medium	Low	Open	Substrate disturbed	Skidder	Slash-pile
Lophocolea heterophylla	50	49	47	27	22	13	5
Ceratodon purpureus	2	0	6	11	5	20	5

Tables Part 2:

Table 1: Species list for 36 quadrats in riparian buffer (2000), and in 1995 pre-harvest quadrats, including their frequency and mean % cover when present. Liverworts are in bold.

Species	Riparian buffer		Pre-harvest (1995)	
Species	frequency	mean % cover when present	frequency	mean % cover when present
Ambylstegium serpens	2	0.13	3	0.15
Anastrophyllum hellerianum	2	0.05	B	-
Aulacomnium palustre	1	6.30	15	1.47
Barbilophozia attenuata	-	-	1	0.05
Bazzania denudata	1	0.05 *	-	-
Bazzania trilobata	6	0.97	20	2.50
Blepharostoma trichophyllum	1	0.17	8	0.06
Brachythecium campestre	2	0.98	6	0.44
Brachythecium erythrorrhizon	1	0.13H	-	-
Brachythecium populeum	1	0.10	5	1.04
Brachythecium reflexum	12	0.67	8	0.20
Brachythecium rivulare	1	0.10H	-	-
Brachythecium rutabulum	8	0.16	21	1.07
Brachythecium salebrosum	3	1.05	23	0.61
Brachythecium starkei	20	0.61	100	0.72
Brachythecium velutinum	5	0.21	9	0.53
Brotherella recurvans	5	2.03	6	1.43
Bryhnia novae-angliae	1	5.37	9	3.64
Callicladium haldanianum	20	0.47	39	1.16
Calliergon cordifloium	1	0.10*H	-	-
Calypogeia integristipula	-	-	1	0.05
Calypogeia muelleriana	1	0.55	3	0.05
Campylium hispidulum	1	0.05	27	0.21
Campylium stellatum	-	-	1	0.05
Cephalozia bicuspidata	11	0.06	5	0.05
Cephalozia lunilifolia	5	0.07	11	0.09
Cephalozia spp.	-	-	3	0.05
Ceratodon purpureus	-	-	1	0.05
Cirriphylum piliferum	-	-	2	3.55
Climacium dendroides	-	-	2	2.35
Concephalum conicum	-	-	1	6.00
Dicranella heteromalla	-	-	1	5.00
Dicranum flagellare	14	0.68	49	0.46
Dicranum fulvum	1	0.05I	-	-
Dicranum fuscescens	7	0.42	39	1.06
Dicranum montanum	18	0.31	21	0.36
Dicranum ontariense	1	0.15	13	1.27

Dicranum polysetum	3	0.51	85	3.87
Dicranum scoparium	24	0.55	94	1.09
Dicranum viride	-	-	3	0.07
Diphyscium foliosum	-	-	1	0.20
Drepanocladus uncinatus	23	0.47	43	0.39
Eurhynchium pulchellum	2	0.13	2	0.80
Frullania brittoniae	-	-	1	0.10
Frullania eboracensis	2	0.18	2	0.05
Frullania oaksiana	2	0.05	2	0.05
Geocalyx graveolens	2	0.05	17	0.17
Gymnocolea inflata	-	-	3	0.12
Herzogiella striatella	4	0.34	1	0.05
Herzogiella turfacea	29	0.25	65	0.53
Hylocomnium splendens	2	0.28	12	4.60
Hypnum fertile	-	-	1	0.05
Hypnum imponens	6	1.85	13	1.82
Hypnum lindbergi	-	-	1	0.60
Hypnum pallescens	20	0.27	60	0.24
Hypnum pallescens var. protuberans	-	-	2	0.20
Jamesionella autumnalis	26	0.58	70	0.35
Jungermannia gracillima	-	-	1	0.05
Lepidozia repens	10	0.26	13	0.52
Leptodictyum trichopodium	-	-	1	0.05
Lophocolea heterophylla	28	0.40	74	0.16
Lophozia heterocolpis	-	-	1	0.10
Mnium hornum	2	0.05	-	-
Mnium spinulosum	9	1.44	1	0.05
Nowelia curvifolia	15	0.88	23	0.06
Oncophorous wahlenbergii	2	0.05	1	0.40
Orthotrichum speciosum	1	0.20H	-	-
Plagiochilla porelloides	-	-	3	2.93
Plagiomnium ciliare	-	-	3	2.33
Plagiomnium cuspidatum	8	0.74	33	1.11
Plagiomnium medium	1	0.05	5	2.22
Plagiothecium cavifolium	7	0.20	3	4.83
Plagiothecium denticulatum	1	0.30*	-	-
Plagiothecium laetum	19	0.35	22	0.12
Plagiothecium latebricola	2	0.15	-	-
Platygyrium repens	3	0.19	4	0.11
Platydictya subtile	-	-	1	0.10
Pleurozium schreberii	20	0.77	117	6.83
Pohlia nutans	1	0.10	6	0.08

Polytrichum commune	1	1.00	19	1.73
Polytrichum juniperinum	-	-	11	1.24
Pseudobryum cinclidioides	1	0.05*H	-	-
Ptilidium cilliare	1	0.25	18	1.53
Ptilidium pulcherrimum	30	0.93	111	0.68
Ptilium crista-castrensis	1	0.05	22	0.89
Pylaisiella intricata	-	-	1	0.50
Radula complanata	4	0.63	-	-
Rhizomnium appalachainum	-	-	3	6.03
Rhizomnium punctatum	3	0.17H	-	-
Riccardia latifrons	-	-	2	0.08
Rhytidiadelphus triquetrus	-	-	6	11.43
Scapania nemorosa	-	-	2	0.28
Sphagnum capillifolium	-	-	1	14.00
Sphagnum fallax	-	-	1	0.30
Sphagnum squarrosum	1	11.00	2	5.20
Sphagnum subsecundum	2	0.15	-	-
Tetraphis pellucida	9	0.34	26	0.45
Thuidium delicatulum	2	4.57	2	0.85
Thuidium recognitum	1	0.05*	6	3.26
Trichocolea tomentalla	-	-	1	0.05
Ulota coarctata	4	0.05I	1	0.05
Ulota crispa	4	0.05	-	-

* species found only in quadrat B-13 only
H species found only in the riparian buffer
I species found only in post-disturbance quadrats

Table 2: Comparison of the riparian buffer bryophyte community (2000) to pre-harvest and post-harvest communities.

Comparison of buffer vs:	Year	Similarity index	MRPP	
			T value	p value
pre-harvest	1995	57.7%	-5.823	0.0014
post-harvest	1999	55.4%	-3.859	0.0096

Table 3: Correlation coefficient (Spearman=s rho) and probability (in brackets) between DCA axis scores of the pre-harvest/buffer (Figure 1) vs diversity indices and buffer quadrat characteristics. Values in bold are statistically significant at Æ 0.05.

	Height above stream	Distance from stream	Distance from edge
Axis 1	**-0.386 (0.027)**	-0.166 (0.357)	0.192 (0.286)
Axis 2	-0.189 (0.293)	-0.150 (0.404)	0.125 (0.488)
richness	**-0.344 (0.050)**	**-0.380 (0.029)**	0.322 (0.068)
evenness	0.144 (0.425)	0.074 (0.682)	-0.108 (0.548)
Simpson=s index	-0.134 (0.457)	-0.153 (0.395)	0.183 (0.308)
total cover	-0.203 (0.258)	-0.237 (0.184)	0.180 (0.315)