Fire and Vegetation in a Temperate Peat Bog: Implications for the Management of Threatened Species

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Abstract: *Fire plays an important role in structuring wetland ecosystems, but previous studies of New Zealand wetlands have lacked adequate experimental controls. We investigated the effects of fire on the vegetation of a New Zealand peat bog through analysis of microclimate patterns, vegetation change, and peat stratigraphy. We focused on the role of fire in sustaining threatened plant species such as the critically endangered orchid* Corybas carsei. *Experimental fire significantly increased the surface radiation and daytime soil temperature, and these elevated levels of radiation and temperature persisted 53 months after burning. Immediately after fire no living plant material remained in the burn plots, but within 2 months many of the rhizomatous species were resprouting and 50 months later had returned to prefire abundance. Obligate-seeding species did not recover their former abundance, but several species not observed in the plots prior to the burns established after fire. Species richness, diversity, and evenness increased following fire but declined in the control plots. Species dominance decreased after fire but increased in the control plots.* C. carsei, *which was killed during the fire, reappeared in the burn plots 1 year later at a higher density than prior to burning and was still present 4 years after fire.* C. carsei *flowering was also enhanced following the fire. We found evidence of historical fires, which was supported by radiocarbon dates from a much older adjacent wetland. Our results suggest that disturbances such as fire are important for maintaining a diversity of plant communities, including the presence of nationally threatened and declining plant species in peat bogs. Without such disturbances species such as* C. carsei *are likely to become locally extinct.*

Incendios y Vegetación en una Turba Pantanosa Templada: Implicaciones para el Manejo de Especies

Resumen: *Los incendios juegan un papel importante en la estructuración de ecosistemas de humedales, pero los estudios previos de los humedales de Nueva Zelanda carecían de controles experimentales adecuados. Investigamos los efectos del fuego en la vegetación de una turba pantanosa de Nueva Zelanda mediante el análisis de patrones microclimáticos, el cambio de vegetación y la estratigrafía de la turba. Nos enfocamos en el papel del fuego en el mantenimiento de especies de plantas amenazadas como la orquídea (*Corybas carsei*) críticamente amenazada. Los incendios experimentales incrementaron significativamente la superficie de radiación y la temperatura diurna del suelo y estos niveles elevados de radiación y temperatura persistieron por 53 meses después de la quema. Inmediatamente después del incendio no quedaba ninguna planta viva en los cuadrantes quemados, pero en cuestión de 2 meses, muchas de las especies rizomatozas estuvieron retoñando por 50 meses y han retornado a la abundancia presente antes del incendio. Las especies de semillas obligadas no recuperaron su abundancia previa, pero varias especies que no se observaban en los cuadrantes antes de las quemas se establecieron después del incendio. La riqueza de especies, la diversidad y la uniformidad incrementaron después del incendio, pero disminuyeron en los cuadrantes control. La dominancia de especies disminuyó después del incendio pero incrementó en los cuadrantes control.* C. carsei, *que había muerto durante el incendio reapareció un año después en los cuadrantes quemados con*

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una densidad mayor que la que tenía antes del incendio y estaba aún presente 4 años después del incendio. También incrementó el número de C. carsei *floreciendo después del incendio. Encontramos evidencias de incendios históricos, lo cual es apoyado por fechas de radiocarbón de un humedal adyacente mucho más viejo. Nuestros resultados sugieren que perturbaciones tales como los incendios son importantes para el mantenimiento de una diversidad de comunidades de plantas, incluyendo la presencia de especies de plantas amenazadas a nivel nacional y en disminución en turbas pantanosas. Sin estas perturbaciones, es posible que especies como* C. carsei *posiblemente se extingan localmente.*

Introduction

Fire and different fire regimes play an important role in structuring natural ecosystems (Whelan 1995; Bond & van Wilgen 1996). Fire can have complex effects on vegetation depending on the timing, intensity, and nature of the fire and on interactions with other disturbance regimes and the physical characteristics of the landscape within which it occurs (Kirkman 1995; Menges & Hawkes 1998). Although fire suppression has been actively pursued in many countries in the past, prescribed fire is now widely used as a conservation tool in areas where natural fire patterns have been modified by human activities (Baker 1994). But such use of fire is complex and often poorly understood, especially with respect to the influence of fires at different temporal and spatial scales (Shinneman & Baker 1997).

Although most of the focus on fire management in conservation has been on grassland, shrubland, and forest ecosystems, natural fires also have a substantial influence on wetland communities (Norton 1989; Kirkman & Sharitz 1994; Gabrey et al. 1999; de Lange et al. 1999*a*; Kost & De Steven 2000). Although these and other studies have emphasized the importance of fire as a tool in wetland management, many wetland restoration and management studies continue to focus on the effects of drainage and biological invasions (Wheeler et al. 1995) rather than on fire. In New Zealand, for example, where fire has been identified as an important influence on wetland composition and structure (Norton 1989; Timmins 1992; Clarkson 1997; de Lange et al. 1999*a*), little attention has been given to the use of fire as a management tool in the conservation of wetland plants and plant communities.

The importance of active wetland management is emphasized by the growing number of species that are declining or have become locally extinct in wetlands (Wilson & Given 1989; de Lange et al. 1991; Kirkman & Sharitz 1994). One reason for our study was a concern that the nationally threatened wetland orchid, *Corybas carsei*, was rapidly heading toward extinction (Clarkson et al. 1993). Our study site was the only known extant site for this orchid and numbers had been declining prior to our research.

Although fire has been found to be important in the ecology of New Zealand wetlands and in the conservation of threatened wetland plants, all previous studies of the response of vegetation to fire in New Zealand wetlands have been based on either chronosequences of historical fires or remeasurements of post-fire vegetation (e.g., Timmins 1992; Clarkson 1997; McQueen & Forester 2000). In both situations there have been no experimental controls against which to compare the responses of vegetation. We used an experimental fire, with burn and control plots, to assess the role of fire as a conservation tool in a New Zealand wetland. In particular, we (1) quantified the response of wetland vegetation to a winter burn and (2) tested the hypothesis that threatened and uncommon plants, including *C. carsei,* are favored by fire.

Methods

Study Area

The Whangamarino wetland is 50 km north of Hamilton City, North Island, New Zealand (lat. 37°22′S, long. 175°9′E, 70 m above sea level). It is a 7106-ha wetland complex, much of which is administered as a reserve. Mean annual rainfall at Te Kauwhata (immediately southwest of Whangamarino) is 1174 mm, with a distinct winter maximum (360 mm in May–July). Mean annual temperature is 14.3° C, with January and July means of 18.7° C and 9.3° C. Frosts and low-lying fogs are common in winter. We worked in the Te Reao peat bog, the southern part of the Whangamarino wetland complex.

Much of the bog vegetation is early to mid-oligotrophic, reflecting the dominance of the Cyperaceous genera *Baumea* (especially *B. teretifolia*), *Schoenus* (especially *S. brevifolius*) and *Tetraria*, which are typical of low-moor bog complexes (de Lange 1989). In the Whangamarino, these species commonly grow interspersed among *Empodisma minus*, the woody shrub *Epacris pauciflora*, and the fern *Gleichenia dicarpa*, species more typical of raised-bog systems (Newnham et al. 1995; de Lange et al. 1999*a*). The Te Reao peat bog is the only part of the Whangamarino wetland known to have supported populations of the critically endangered orchid *C. carsei* and vulnerable clubmoss *Lycopodiella serpentina* (threatened plant classification follows that of de Lange et al. [1999*b*]). The acid-favoring bryophytes *Campylopus acuminatus* var. *kirkii* and *Goebelobryum unguiculatum* are also common in this area. These species are characteristic of oligotrophic high-moor bog complexes, where they occupy sites kept open through the extreme acidity of the peat (Newnham et al. 1995). The wetland is bordered by mesic-eutrophic swamps and *Salix* woodland (Ogle & Bartlett 1981).

Much of Te Reao is bounded by intensively farmed low-lying hill country, and the main trunk railway line delineates the western margin. During most of the twentieth century, fires originating from land clearance, weed control, and steam engine sparks frequently swept across the bog (Reeves 1994; D. K. Lloyd, personal communication). As a result, the vegetation of Te Reao at that time comprised a rich mosaic of vegetation types at different post-fire successional stages in which the open, moss-covered ground favored by species such as *C. carsei* was prevalent. Since 1960, however, fires on Te Reao have virtually ceased, the most recent occurring in 1973 (Reeves 1994). More recently, active fire suppression has become policy for the agency managing the land (Timmins & Hillard 1998). Following the reduction in fires, the vegetation of Te Reao shifted from a diverse mosaic of vegetation types to one dominated by tall *Baumea* and *Schoenus* sedges, *G. dicarpa*, *E. pauciflora*, and *E. minus* (B. P. J. Molloy and D. K. Lloyd, personal communication). In particular, the contraction of open, moss-covered sites led to a marked decline in *C. carsei* and *L. serpentina*, such that by 1991 only 30 individuals of *C. carsei* were known. *L. serpentina*, which had been considered abundant in the area in 1982–1983 (C. C. Ogle, personal communication), was thought to have become locally extinct (P. J. d. L., unpublished data).

Data Collection

To reduce the potential for development of an uncontrolled fire, we were permitted to undertake one winter burn in 12 plots no larger than 2 m^2 each. Accordingly, 24 permanent 2 × 2 m plots (12 controls and 12 burns) were established in three areas of Te Reao in 1994 (8 randomly located in each area). The dominant vegetation in the three areas was similar, but the areas differed in the status of *C. carsei*, which was (1) present, (2) present historically (based on records of the last 20 years), or (3) absent (never known to have been present).

Each fire was started with a hand-held propane gas burner and was contained within the prescribed 2 × 2 m area by a corrugated iron fence. All fires were ignited and extinguished on 13 July 1994. Winter in these peat bogs is cool and wet, and a light frost was present across the bog on the morning of the burn. These conditions resulted in a "cool" burn; in particular, the underlying peat did not ignite as it does during a typical summer burn. Uncontrolled burns in this peat bog, similar to ours, have been recorded (Clarkson 1997).

We randomly located two microclimate sample points in four of the plots in the orchid-present area (two controls and two burns). At each sampling point we measured (1) incident photosynthetically active radiation (PAR) with a LiCor LI190SB quantum sensor 0.1 m above the ground surface and (2) soil temperature with a Campbell 107B temperature probe at 0.1 m depth. We took measurements at 10-second intervals, stored as 30-minute averages, with Campbell 21X and CR10 data loggers. Microclimates were measured simultaneously at all four plots for 6 days on four occasions: (1) immediately prior to the fire in July 1994, (2) immediately after the fire in July 1994, (3) February 1995, and (4) December 1998. We also took spot readings of temperatures during the fires with a high-temperature probe.

Prior to the burn and immediately after, we measured the pH and organic content of peat samples. The pH was measured in water extracted from the peat by squeezing. Organic content was based on loss-on-ignition and involved combusting an air-dried peat sample at 600° C for 12 hours then weighing the resultant ash.

Immediately prior to the burns (14 July 1994), the cover abundance of all species of vascular plants, bryophytes, and lichens was recorded in each plot. These measurements were repeated 13 days after the burn and again in September and November of 1994; February, March, June, September, and December of 1995; February and August of 1996, February and October of 1997, and April and September of 1998. We initially conducted sampling at intervals of 2–3 months to follow the initial response of vegetation to burning, then twice yearly to include species such as orchids that are seasonally dormant (in summer). Individual plants of *C. carsei* found within the study plots were tagged, and flowering and fruit set in the burn plots were recorded at each visit. The vegetation of the control plots was examined only prior to the fire and at the conclusion of the experiment (September 1998) to reduce the risk of our disturbing it by searching among the dense mat of plant material for ground plants. Such disturbance enhances the growth of plants such as *C. carsei* (Clarkson et al. 1993). In contrast, the vegetation of the burned plots was still sufficiently open at the end of the experiment to enable us to assess vegetation abundance without affecting it. Although we did walk around both burned and control plots, we did not walk in any of the plots themselves. We took final measurements in September (spring) of 1998 because summer-dormant species were still abundant at this time, species that would have been present during the original July measurement. For logistical reasons we were unable to access the bog in July and August 1998.

Data Analysis

We used repeated-measures analysis of variance (ANOVA) to compare peat pH and organic content from immediately before to immediately after the fire. Climate data were summarized to produce three sets of daily values based on the 30-minute climate measurements of mean daytime soil temperature and PAR and mean nighttime soil temperature. We defined daytime as 1130–1530 hours and nighttime as 2330–330 hours. We assessed differences between the burn and control plots using ANOVA for the four climate-measurement time intervals (July 1994 before, July 1994 after, February 1995, December 1998). In these analyses the individual days were treated as the repeated measure and the four time intervals were analyzed separately.

To identify changes in community composition with time, we ordinated the floristic data collected from the 24 plots at each sample time with detrended correspondence analysis as implemented in CANOCO (ter Braak & Smilauer 1998). Cover scores for each species were averaged from the four plots of each treatment prior to analysis. This meant that for the first and last measurements (July 1994 before fire and September 1998) there were six data sets (three treatment sites and three control sites), and for the 13 measurements in between there were three data sets (one for each of the treatments).

We compared vegetation composition from before the burn (July 1994) to 4 years later (September 1998) by using four indices of diversity: species richness, Shannon-Wiener diversity, Shannon evenness, and Berger-Parker dominance (Magurran 1988). We then assessed differences in these indices and total foliage cover between the burn and control plots using ANOVA. We compared measurements made in July 1994 before fire and in September 1998 because summer-dormant species are present from May through October, when rainfall is higher and temperatures lower. We used a Fisher's exact test to test the association between the number of *C. carsei* plants flowering and those setting seed across the study years.

Except for the ordination, analyses followed procedures in the Statistical Analytical System (version 8). We checked all data for normality prior to analysis and transformed them as appropriate.

Peat Stratigraphy and the Historical Fire Record

To ascertain the development and paleofire history of the study area, we sampled three 5- to 5.5-m cores from the vicinity of the burn plots. We took cores using a Russian-Jowsey D-section corer and made notes on the nature of the peat deposits, the presence of distinctive marker horizons and charcoal layers, and identifiable macrofossils. Four samples spanning the main changes in peat stratigraphy were taken from one core and submitted for radiocarbon dating at the University of Waikato Radiocarbon Dating Laboratory, Hamilton, New Zealand. All ages are reported as conventional radiocarbon ages based on the Libby half-life of 5568 years.

Results

Fire

The cool burns removed all surface vegetation, but it appears from a lack of evidence of peat burning that little or no fire penetrated the peat. Although air temperatures in the path of the flame exceeded 700° C, surface temperatures rarely exceeded 300° C. Compared with the control plots (mean values are presented with standard errors), organic content decreased significantly (96.2 ± 0.5% before, 93.5 ± 0.9% after, $p = 0.024$) and pH increased significantly (4.8 ± 0.1 before, 6.3 ± 0.4 after, $p = 0.015$) after fire in the burn plots, with the change being greatest for pH. There was no change in these parameters in the control plots.

Microclimates

Statistical analysis of microclimate data was not possible for the before-fire measurements because of the failure of some sensors. Usable PAR data collected prior to the burn were available for one burn and one control plot only, but daytime PAR averages were similar (Table 1). In contrast, daytime PAR immediately after the fire treatments was much higher in the burn plots than in the control plots. In February 1995 and December 1998, daytime PAR was significantly greater in the burn plots than in control plots (Table 1). Prior to the burn, soil temperature at 0.1 m showed only minor variation, ranging between a minimum of 4.5° C and a maximum of 8.6° C, with no obvious difference between burn and control plots (Table 1). In contrast, immediately after the fire treatment, daytime soil temperature was much higher in the burn plots than in the control plots, and these differences were significant in February 1995 and December 1998. Nighttime temperatures were not significantly different between the burn and control plots at any of the measurement times (Table 1).

Vegetation

Immediately after the fire, no living plant material remained above ground level in the burn plots. Two months later, however, many of the rhizomatous species were resprouting (e.g., *S. brevifolius*), and several adventive species (introduced to New Zealand since European settlement), especially *Salix cinerea*, became es-

Table 1. Microclimate conditions (± SE) in burn and control plots at four different times, and repeated-measures analyisis of variance *p* values for the difference between burn and control plots.*

	Burn	*Control*	p
Ground-level photosynthetic active radiation (μmol/m^2/sec)			
1994 before	7.2 ± 1	11.8 ± 2	—
1994 after	538 ± 72	6 ± 1	0.067
1995	1089 ± 104	87 ± 21	0.012
1998	568 ± 114	28 ± 3	0.003
Substrate daytime temperature (° C)			
1994 before	7.5 ± 0.4	7.5 ± 0.4	—
1994 after	11.2 ± 0.3	8.3 ± 0.3	0.056
1995	27.8 ± 0.7	17.8 ± 0.2	0.014
1998	32.0 ± 2.2	27.0 ± 1.1	0.039
Substrate nighttime temperature (° C)			
1994 before	7.1 ± 0.5	6.7 ± 0.6	—
1994 after	8.2 ± 0.4	8.0 ± 0.4	0.917
1995	17.2 ± 0.2	17.4 ± 0.1	0.798
1998	11.7 ± 1.6	12.1 ± 0.9	0.684

**Except for "1994 before," for which there was no sensor replication.*

tablished over the first summer (Fig. 1). By the end of the first summer, most plots were dominated by sundews (*Drosera* species), with small patches of *Lycopodiella lateralis* and the bladderwort *Utricularia delicatula* present. By the second summer, the majority of the adventive species had died out, and *L. lateralis*, *U. delicatula*, and *Campylopus* were slowly spreading at the expense of *Drosera binata* (Fig. 1). Many of the obligate-seeding species (e.g., *Leptospermum scoparium*, *E. pauciflora*, and *E. minus*) were also present in the plots, although for the duration of the study these species never recovered their former abundance (Fig. 1). In marked contrast, all the rhizomatous species returned to their prefire abundance by the end of the experiment (Fig. 1).

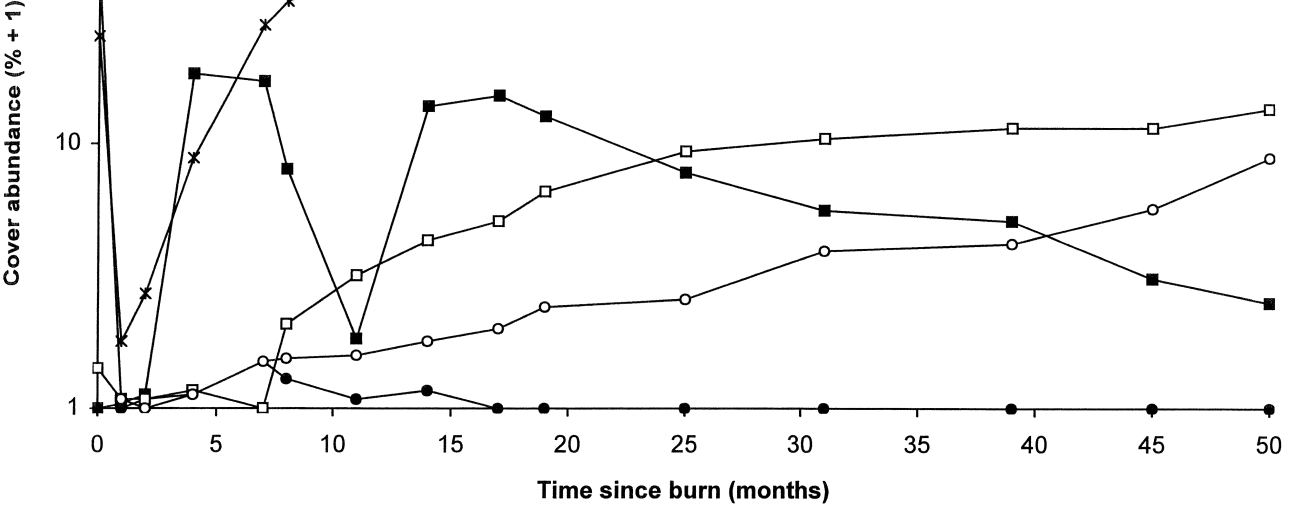

Figure 1. Changes in the abundance of selected species with time after fire (a full list for all species is available from the authors upon request).

Explained variance was high on the first ordination axis (40.8%) but low on the second (10.9%). Species turnover on both axes (2.6 and 2.2 SD units, respectively) indicated a >50% change in sample floristic composition (sensu Hill & Gauch 1980) along each axis. The first axis of the site ordination (Fig. 2) separated the before-fire measurements and control plots from all post-burn measurements. The second axis provided some separation of measurements made at different times, with the most recent measurements (1997 and 1998) tending to have lower axis 2 scores than the earlier measurements (1994 and 1995). The three measurements with the highest axis 2 scores were the summer measurements of 1994 and 1995. The July 1994 and September 1998 control plots showed no difference in ordination position (Fig. 2). Plant species with low scores on the first axis of the species ordination included *L. scoparium*, *E. pauciflora*, *E. minus*, *Ptychomnium aciculare*, *Cladonia* species, *Ramalina celastri* subsp. *celastri*, and *Usnea arida*, all species typical of unburned plots. Species with high scores on axes 1 and 2 included the adventives *Cirsium arvense*, *Hypochaeris radicata*, *S. cinerea*, and *Senecio bipinnasectus*, which appeared during the first summer after the fire but did not persist. The native species *Euchiton involucratus*, *D. binata*, *L. serpentina*, and *Thelymitra cyanea*, which are favored by the open conditions after fire, also had high scores on axes 1 and 2. Species such as *C. carsei*, *B. teretifolia*, *S. carsei*, and the *Utricularia* species, which had low scores on axes 1 and 2, were still increasing in abundance in the burn plots at the end of the study.

All four diversity indices and total foliage cover were significantly different than the controls from before to 4 years after the fire (Table 2). Average species richness in individual plots increased from 7.8 ± 0.6 to 14.3 ± 0.8 species with fire, whereas average species richness in the control plots declined from 8.9 ± 0.6 to 6.3 ± 0.3 species. Diversity and evenness also increased with fire but decreased without fire, whereas dominance decreased after fire and increased in the control plots. Total foliage cover, although zero immediately after the fire, was significantly greater 4 years after fire than prior to the fire. However, total foliage cover decreased in the control plots over the study period.

Five nationally threatened and uncommon plant species (*C. carsei*, *L. serpentina*, *Prasophyllum* aff. *patens* [vulnerable]; *S. carsei* [nationally declining]; and *Pterostylis paludosa* [nationally declining]) were recorded in the burn plots during the study. Only two of these (*C. carsei*, *P. paludosa*) were present prior to the burns, both at low levels. All five species responded positively

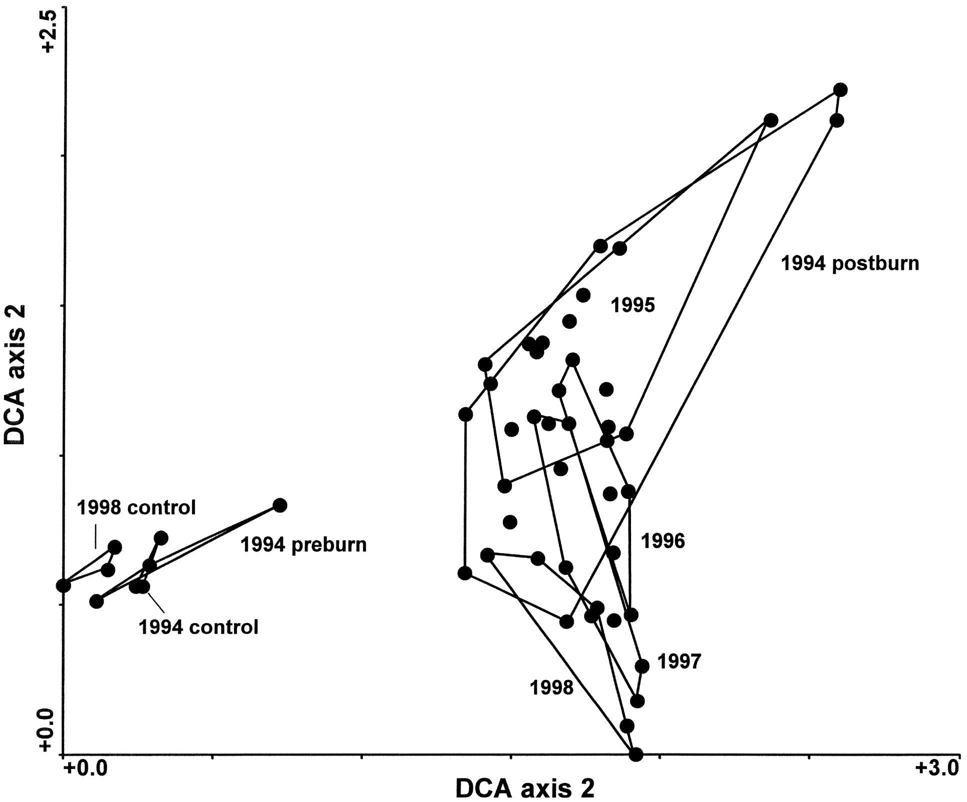

Figure 2. Detrended correspondence analysis (DCA) ordination of vegetation plots sampled at different times, plotted with lines enclosing plots sampled in the same year.

Table 2. Diversity index and vegetation cover (± SE) before and 4 years after the fire for burn and control plots, with repeated-measures analysis of variance *p* values.

				p		
Index	*Treatment*	*Before*	*After*	*fire*	*time*	*time*fire*
Species richness	fire	7.8 ± 0.6	14.3 ± 0.8	0.001	0.005	0.001
	no fire	8.9 ± 0.6	6.3 ± 0.3			
Diversity	fire	1.270 ± 0.072	2.045 ± 0.107	0.001	0.001	0.001
	no fire	1.280 ± 0.065	1.040 ± 0.083			
Evenness	fire	0.636 ± 0.038	0.769 ± 0.033	0.008	0.083	0.006
	no fire	0.596 ± 0.034	0.563 ± 0.038			
Dominance	fire	0.510 ± 0.042	0.335 ± 0.032	0.013	0.166	0.001
	no fire	0.504 ± 0.040	0.588 ± 0.043			
Total cover	fire	102.4 ± 1.8	171.4 ± 14.1	0.001	0.001	0.001
	no fire	103.6 ± 1.5	99.9 ± 0.9			

to the experimental burns (Fig. 3), although two species were declining in cover abundance (*C. carsei*, *P. paludosa*) by the last measurement.

The more detailed assessment of *C. carsei* showed that this species was present in all eight plots (four control and four burn) in the orchid-present area prior to the fire. The aboveground parts of *C. carsei* were killed by the experimental fires, and the species remained absent from the burn plots for the rest of 1994 (Fig. 4). In 1995 *C. carsei* reappeared in the burn plots at a higher density than before the fire (21.8 ± 17.8 plants/plot after fire and 7.3 ± 5.3 before fire). Density peaked 2 years after the fire, at 75.3 ± 55.7 plants/plot, and declined over the next 4 years to 13.7 ± 7.7 plants/plot. *C. carsei* was not visible in the control plots 6 years later. *C. carsei* did not reappear in any of the burn plots in the orchid-historical area. However, it did appear in one of the burn plots in the orchid-absent area 4 years after the fire (Fig. 4) and then increased in abundance (4.5 ± 4.5 plants/plot 6 years after the fire).

Prior to the experimental fires, only one *C. carsei* plant had been observed to flower in the study area, and it did not set seed (P.J.d.L., unpublished data). Flowering was induced after fire, although seed set was limited (Fig. 5). There was no significant difference in the proportion of plants that flowered among years ($p = 0.954$), but there was a significant difference in the proportion of flowering plants that set seed among years ($p = 0.003$), with seed set significantly higher than expected in 1997 (Fig. 5). The July 2000 visit was too early in the

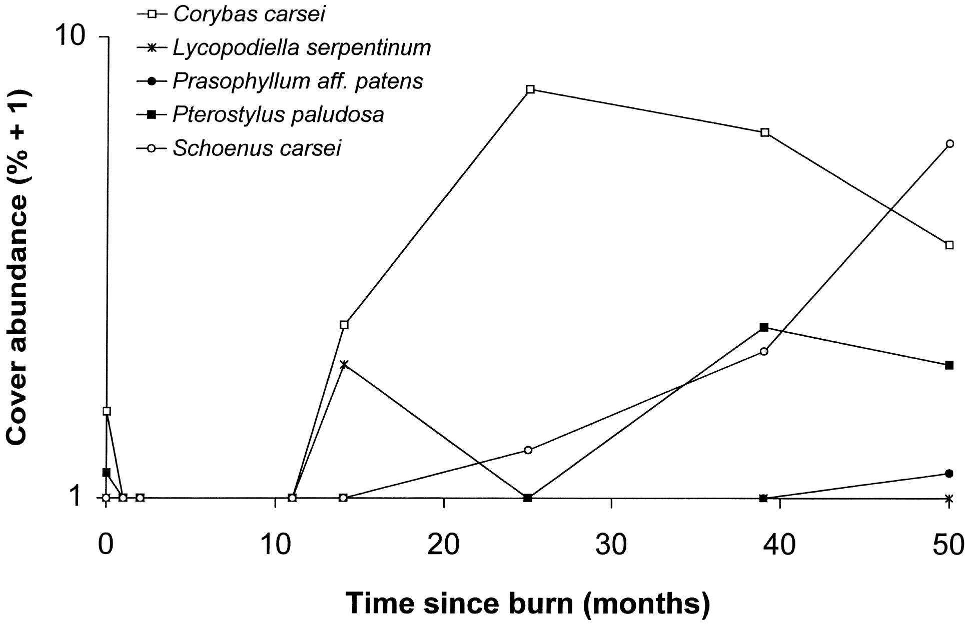

Figure 3. Changes in the abundance of nationally threatened and declining plant species with time after fire. Only winter/spring measurements have been included because some of these species are dormant in summer/autumn.

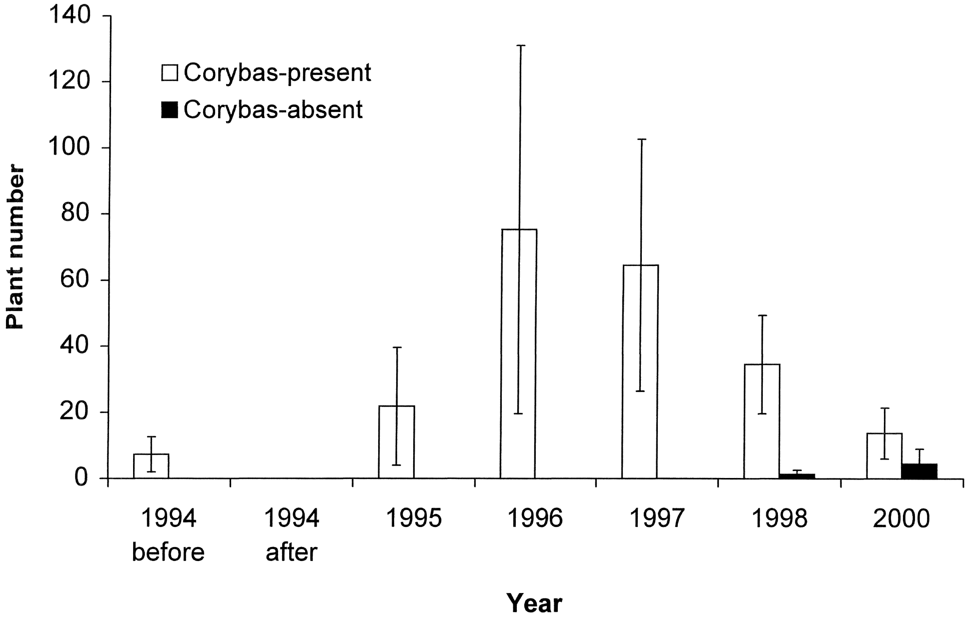

Figure 4. Mean number (± SE) of Corybas carsei *plants in the orchid-present and orchid-absent plots for winter/ spring measurements (May-October).* C. carsei *was not recorded from the orchid-historical plots.*

season for assessment of flowering and seed set, although buds and some flowers were present.

Peat Stratigraphy and the Historical Fire Record

All three peat cores showed a similar pattern. The basal peat deposits (dated at 5640 ± 200 years before the present, Wk-8577) were highly vesiculated and decomposed, and the plant macrofossils present (e.g., *Typha orientalis* and *Phormium tenax*) suggested that lacustrine/ eutrophic conditions were present at this time. A much younger *Dacrycarpus dacrydioides* peg root (1310 ± 200 years before the present, Wk-8578) below this peat probably arose from trees growing adjacent to the bog. From 4 to 2.5 m the sediments were too fluid to sample. From 2.5 m to the surface the cores all showed a distinct, although gradual, change from an extremely decomposed, brown, highly organic fluid to an increasingly fibrous brown peat. From 1.9 m the cyperaceous genus *Baumea* (mainly *B. rubiginosa*) and *G. dicarpa* were present, suggesting middle to late mesotrophic conditions. From 1.5 to 0.5 m, *Baumea* macrofossils dominated, suggesting early oligotrophic conditions. At 0.5 m the first definite macrofossils of the restiad *E. minus*, moss *C. acuminatus* var. *kirkii*, and clubmoss *L. latera-*

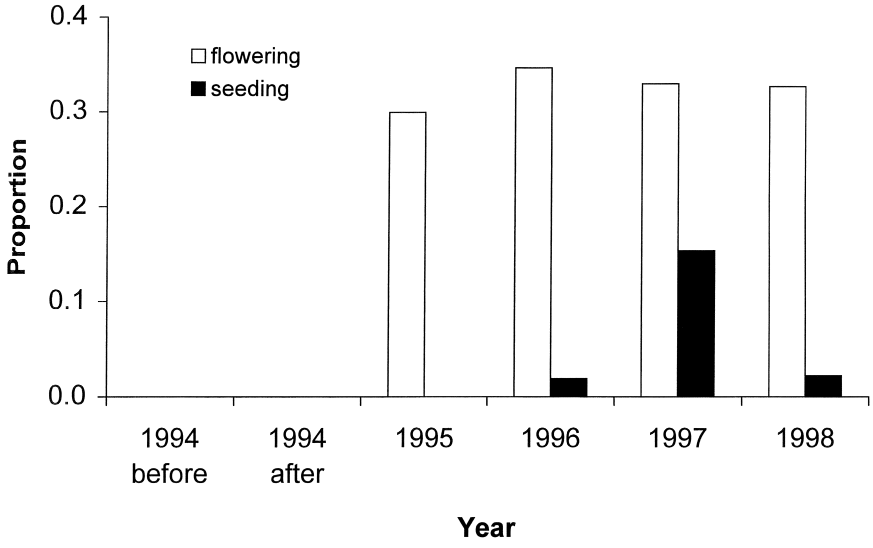

Figure 5. Proportion of Corybas carsei *plants flowering and of flowering plants setting seed in the burned plots at the orchid-present site (summed for four plots).*

lis became evident, and the sedges *S. brevifolius* and *B. teretifolia* become the dominant cyperaceous species. These species are typical of the early to middle oligotrophic conditions that occur in the bog today. Radiocarbon ages obtained from samples Wk-8575 (0.2 m) and Wk-8576 (0.9 m) provided "modern" ages (<200 years before the present) for these recent changes, suggesting that the onset of full oligotrophic conditions occurred sometime within the last few hundred years. Seven charcoal layers were observed in the upper 0.7 m of the cores, and evidence for two further fire events at 2.45 and 1.5 m was also found. However, the sediment present through this part of the cores was not conducive to charcoal preservation.

Discussion

Fire and Peat-Bog Vegetation

The experimental burns resulted in a significantly greater species richness, evenness, and diversity of plant species 4 years after the fire than in the control plots. In contrast, these variables decreased in the control plots over the 4-year study. Dominance showed the opposite pattern. An initial increase in diversity after fire has been widely observed in studies of vegetation response to fire, but diversity values usually return to pre-burn levels with time (Whelan 1995). Increasing species richness after fire in other New Zealand wetlands has also been observed (Timmins 1992), although over longer time periods species richness appears to decline (Clarkson 1997). The decrease in species-diversity indices in the control plots over our 4-year study suggests that the vegetation in the study area may still be adjusting after earlier fires.

Foliage cover data also suggest ongoing post-fire adjustment in the vegetation, with significantly higher foliage cover in the burned plots than in the control plots. In an earlier study at Whangamarino and in another Waikato wetland, vegetation took 5.5 and 11.5 years, respectively, to reach preburn cover (Clarkson 1997). In a bog dominated by *Sphagnum* and *E. minus*, total plant cover reached 90% of the prefire cover within 4.5 years (Timmins 1992), whereas in a bog dominated by *Schoenus* and *Leptospermum* vegetation returned to prefire cover 10 years after fire (McQueen & Forester 2000). In North American sedge meadows, vegetation cover similar to preburn conditions occurred after 7 years (Kost & De Steven 2000).

As is common with other studies of vegetation response to fire (Kirkman & Sharitz 1994), the pattern of species recovery after fire was strongly influenced by the life history and morphological attributes of the burned species. Species establish after fire by sprouting either from regenerative organs such as rhizomes or from seed, which may either be present in the peat, in remnant vegetation, or subsequently dispersed into the burned site. For example, of the rhizomatous species present, the sedge genera *Baumea* and *Schoenus* and the fern *G. dicarpa* recovered steadily after fire because they resprouted from underground rhizomes. Other species, such as *E. minus* and *E. pauciflora*, were completely killed by the fires such that subsequent recolonization was from seed dropped by mature plants adjacent to the plots; these taxa had not regained prefire abundance levels 4 years after the fire.

The presence of charcoal layers in the peat at our study site and in the much older (by about 12,000 years) Kopouatai Bog (Newnham et al. 1995), 35 km east of Whangamarino, support the existence of fire as an important natural-disturbance regime in these peat bogs. At Kopouatai fires occurred once every 100–244 years in the 5000 years prior to human settlement. Although our radiocarbon dates provided evidence of several fires in the last 200 years, there was also evidence of older fires from undated charcoal layers, despite the sediments not being conducive to charcoal preservation.

The importance of fire in New Zealand ecosystems has not received as much attention as it has in other parts of the world, but there is growing evidence that natural fire has played a role in shaping community composition and structure in many parts of New Zealand (Ogden et al. 1998). Although fire seems an unlikely disturbance regime in wetlands, the presence of charcoal in wetland sediments and current vegetation patterns strongly suggest that natural fires have influenced the composition and structure of wetland communities in New Zealand (Norton 1989; Newnham et al. 1995) and elsewhere (Kirkman & Sharitz 1994; Gabrey et al. 1999; Kost & De Steven 2000). Tall rush, sedge, and restiad plants provide a suitable fuel source for fire because of their tendency to dry out during periods of low rainfall, which facilitates the spread of fire, as highlighted by the recent abundance of anthropogenic fires (e.g., Williams et al. 1990; Timmins 1992; Clarkson 1997; McQueen & Forester 2000).

Fire and Threatened Species

Our results clearly show that fire provides conditions suitable for both vegetative and reproductive growth of threatened plant species such as *C. carsei,* and they confirm the observations of Carse (1926) and Butcher (1965), who suggested that *C. carsei* benefits from disturbances such as fire. In the absence of fire, however, *C. carsei* continued to decline; in our unburned plots at least, this species appeared to become locally extinct. It is unclear whether fire completely kills *C. carsei* plants or if the buried tubers survive. In our burns, peat temperatures were not high, so tuber survival, especially at depth, is a possibility. But the slow reappearance of *C. carsei* plants after fire does suggest some seed dispersal from outside our burn plots. This suggestion is supported by the failure of *C. carsei* to become reestablished after fire at Moanatuatua, a floristically similar peat bog (Clarkson 1997), despite it having been very common there 10 years prior to that fire (Butcher 1965).

Fire also appears to have provided optimal conditions for *C. carsei* flowering. At Te Reao, despite regular study (Clarkson et al. 1993), *C. carsei* was observed to flower only once before fire, yet it flowered vigorously after fire. Enhanced reproductive success after fire disturbance is often observed (Bond & van Wilgen 1996; Kirkman et al. 1998) and reflects increased resource availability and reduced competition after fire. Fire does not appear to have directly stimulated flowering in *C. carsei* because peak flowering occurred 2 years after fire. However, enhanced substrate nutrient levels resulting from fires may be an important stimulant for flowering in nutrient-poor wetlands such as Whangamarino. The increase in pH after fire suggests that such a nutrient increase did occur, although experimental nutrient trials would be required to confirm this.

Four other nationally threatened and declining species present at Whangamarino (*L. serpentina*, *P.* aff. *patens*, *P. paludosa*, *S. carsei*) also benefited from fire. As has been observed elsewhere (Gross et al. 1998; Pendergrass et al. 1999), fire created conditions suitable for the occurrence of these species, conditions that did not occur in the absence of fire (de Lange et al. 1991). It therefore seems reasonable to assume that at least one factor in their decline has been an absence of fire. This response of threatened species to fire is similar to that shown by threatened species more generally to disturbance and emphasizes the importance of understanding the disturbance ecology of threatened species in their conservation (Pavlovic 1994).

Implications for Future Peat-Bog Management

A system that experiences a range of fires of different scales and intensities is likely to support a greater overall floristic diversity than a system with few or no fires (Whelan 1995; Bond & van Wilgen 1996). Fire frequencies initially increased after human settlement of New Zealand (Ogden et al. 1998), but they have been substantially reduced more recently as fire-suppression policies have been implemented (Timmins & Hillard 1998). Our results and the limited information available on long-term trends in plant-species abundance from other studies (de Lange et al. 1991; Clarkson et al. 1993; C. C. Ogle, personal communication) suggest that for some threatened and uncommon plant species these changing fire frequencies have resulted in declines and even local extinction. Although fire can benefit some species, it can also have negative effects. Too-frequent fire will lead to a reduction in overall species richness because the chances for reestablishment after fire decrease as the fire frequency and area burned increase, whereas fire can result in an increase in the number of exotic plant species. For example, de Lange et al. (1991) observed that although fire resulted in a proliferation of threatened orchids in a northern New Zealand wetland, it also hastened the spread of seeds of the invasive exotic woody plants *Hakea* and *Acacia*.

Our results show that the vegetation was still responding to fire 4 years after the burns, with floristic composition and vegetation structure still substantially different from preburn conditions. For the critically endangered *C. carsei,* differences between burned and unburned plots were still apparent 5 years after fire, suggesting that fire-return times of >5 years may be sufficient to maintain this species. However, there are still a number of unanswered questions about the way this species and other uncommon species respond to fire. For example, what would have been the response if our burns had occurred in summer or if they had been more extensive? Given these uncertainties, it is important that the use of fire as a conservation tool be undertaken in an adaptive manner in which appropriate feedback from the monitoring of results informs subsequent management actions.

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