Effects of disturbance on population dynamics of the threatened orchid *Prasophyllum correctum* D.L. Jones and implications for grassland management in south-eastern Australia

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ABSTRACT

Natural and anthropogenic disturbances can have dramatic consequences for population growth, particularly for small populations of threatened plants. We analysed census data for the largest population (124 individuals) of the critically endangered orchid *Prasophyllum correctum* between 1992 and 2003, to identify environmental factors associated with annual changes in emergence and flowering, and to develop management prescriptions for its conservation. Fire frequency effects were analysed by comparing life stage transition matrices between plants subject to <3 year and >3 year fire intervals; climate effects were investigated using cross-correlation plots to relate total emergence, and numbers of sterile and flowering plants to rainfall, and grazing impacts were investigated by experimentally protecting plants in 1996–1998. Plants rarely emerged for more than two consecutive years or flowered for more than a single year. The total number of plants that emerged was significantly negatively correlated with autumn/winter rainfall in the previous year, perhaps due to on-going competitive effects of increased grass growth under wetter conditions. The proportion of reproductive adults was greater when fire intervals were <3 years, and a greater proportion of the population remained dormant and non-reproductive when fire intervals exceeded 3 years. Grazing had a significant negative effect on the orchid population in the first 2 years after fire. A management regime that includes frequent burning is likely to benefit conservation of the population by reducing competition from grasses, shortening dormancy periods, reducing mortality, enhancing flowering and, by implication, possibly increasing recruitment.

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1. Introduction

Orchids represent a large proportion of plants at risk in Australia, comprising 10% of rare or threatened species in Victoria (Backhouse and Cameron, 2005). Many endangered orchids have extremely small population sizes (<100 plants), and their in situ conservation poses a major challenge to conservation management agencies.

Large variations in population size in terrestrial orchids are widely reported in the literature, and irregular patterns of emergence, flowering and fruiting appear to be commonplace, at least in the northern hemisphere (e.g., Tamm, 1972; Hutchings, 1987; Gregg, 1991; Light and MacConnaill, 1991; Falb and Leopold, 1993; Kindlmann and Balounová, 1999; Brzosko, 2002). Typically, terrestrial orchids may remain dormant for one or many years and may emerge from dormancy in either a vegetative or flowering state, although only a limited proportion of the plants emerge above ground annually. Few published studies exist on the population dynamics of orchids in Australia. However, observations and unpublished data (Department of Sustainability and Environment, Victoria) indicate that the size and density of many populations fluctuate occasionally or regularly, often in response to environmental disturbance events (e.g. Barnett, 1984; Calder et al., 1989; Cropper et al., 1989).

Fire, herbivory and climate can affect plant populations at both landscape and local scales. Interactions between large- and small-scale environmental impacts are inevitable at the site level and are particularly important where they affect small populations of threatened species. Fire in particular has been a major force in shaping the current composition and structure of Australian vegetation by consuming plant biomass and stimulating flowering, resprouting and germination (Gill, 1981; Auld and O'Connell, 1991; Whelan et al., 2002; Thomas et al., 2003). Prior to European settlement, fires originated from lightning strikes or were deliberately lit by Aborigines (Bowman, 1998; Kershaw et al., 2002). In contemporary times however, natural resource managers have attempted to re-establish ecological fire regimes to maintain and enhance biodiversity values (Keith et al., 2002). A number of studies have demonstrated that fires promote flowering in orchid populations, including *Calopogon multiflorus* Lindl. and *C. pallidus* Chapm. in Florida; *Corybas carsei*, *Prasophyllum* aff. *patens*, *Thelymitra cyanea* and *Pterostylis paludosa* in New Zealand, and *Thelymitra epipactoides* F. Muell. in south-east Australia (Calder et al., 1989; Goldman and Orzell, 2000; Norton and De Lange, 2003).

Grazing by animals can also have a profound effect on orchid population dynamics. The removal of buds and shoots can significantly influence emergence and flowering and a reduction in photosynthetic area in one year may render plants unable to assimilate sufficient carbon reserves to flower in the subsequent year (Whigham and O'Neill, 1991; Brzosko, 2002; Gregg, 2004). The severity of grazing is also important. For example, Gregg (2004) found that a moderately grazed population of *Cypripedium reginae* Walter recovered significantly faster than a heavily grazed population in terms of equilibrium proportions of life states, flowering and plant size.

Some orchid populations respond to variation in annual rainfall, with reduced flowering after drought in the same or previous year (Wells, 1981; Inghe and Tamm, 1988; Wells and Cox, 1991; Light and MacConnaill, 1991), and enhanced flowering following periods of higher rainfall (Hutchings, 1987; Light and MacConnaill, 1991; Sieg and King, 1995; Kéry and Gregg, 2004). Flowering behaviour can be influenced by interactions between rainfall and temperature, site-specific characteristics and seasonal variation within years (Light and MacConnaill, 1991; Sieg and King, 1995; Wells et al., 1998).

Orchid population dynamics are also affected by habitat management, particularly where management activities remove competing vegetation. Removal of plant biomass by mowing, burning, grazing or artificially creating canopy gaps affects orchid population dynamics, mainly by promoting greater leaf area, flowering and seed set but also by creating an open, more suitable environment for seedling establishment (Hutchings, 1987; Waite and Hutchings, 1991; Kull, 1995; Hutchings et al., 1998; Wheeler et al., 1998; Cropper et al., 1989; Willems and Melser, 1998; Willems et al., 2001; Wotavová et al., 2004).

P. correctum (gaping leek orchid) is an endangered terrestrial orchid restricted to two small populations in Victoria, Australia. The largest population occurs in a small grassland remnant that has historically been subject to frequent burning and little grazing. The recovery strategy for *P. correctum* aims to increase population size, mainly through habitat management, by manipulating fire regimes (Coates et al., 1999). However this strategy requires considerable information on the influence of seasonal climatic variations, burning and other disturbances, on the orchid's population dynamics.

Plant demographic studies are useful tools for understanding and predicting population behaviour and for evaluating the response of orchid populations to exogenous influences, particularly management (Waite, 1989; Hutchings, 1990; Shefferson et al., 2001; Kéry and Gregg, 2003, 2004). In this study, we used demographic census data to: (i) quantify patterns of appearance of life stages and plant performance in the largest *P. correctum* population and determine if they are autocorrelated and cyclical; (ii) compare the effect of two different fire frequencies on population dynamics; (iii) evaluate whether rainfall and grazing have a significant influence on plant emergence, flowering and size, and (iv) recommend a management regime to enhance the orchid's conservation and maintain grassland plant diversity. Given the general ecological recognition of the need for regular biomass removal to maintain plant densities in productive grasslands (Grime, 1973; Connell, 1978; Collins et al., 1999; Burke and Grime, 1996; Julita and Grace, 2002; Lunt and Morgan, 2002) and the history of regular burning at the site where the largest *P. correctum* population occurs, we hypothesised that frequent disturbance would be necessary to promote recruitment, emergence, flowering and plant survival.

2. Methods

2.1. The species

P. correctum is a critically endangered orchid (*sensu* IUCN 2000), consisting of fewer than 150 plants known from only two populations in south-eastern Australia. It has a single terete leaf that grows to about 30 cm tall with 10–20 greenish

flowers arranged in an erect spike (Backhouse and Jeanes, 1995). *P. correctum* is a winter-green species and remains dormant during the summer months, when the plant dies back to a single tuber, which is replaced annually prior to initiating shoots which emerge in late autumn (Backhouse and Jeanes, 1995). Plants flower in spring (late October) and seed matures at the end of spring in late November. The orchid is a nectar rewarding species, apparently pollinated by a wasp (observations suggest Ichneumonidae) and like other *Prasophyllum* species is thought to reproduce almost entirely by seeds (Jones, 1998; Backhouse and Jeanes, 1995). Fruit set has been observed annually and 85% of seeds are viable (Huynh, 1999).

2.2. Distribution and study site

When this study began, 54 *P. correctum* plants were known from the larger of two populations, at the Munro rail reserve. Only four plants were recorded at another site, Lindenow South. This study is concerned only with the Munro population.

At Munro, the *P. correctum* population occurs in a remnant *Eucalyptus tereticornis* woodland with a grassy understory dominated by *Themeda triandra*, vegetation which occurred throughout the East Gippsland region prior to European settlement (Lunt, 1997). The region is now highly developed for agriculture, and only small remnants of native vegetation remain, none in a pristine state. The Munro rail reserve study site (37°54′ S, 147°14′ E) is at an altitude of 60 m a.s.l. and experiences a mean annual rainfall of 637 mm, with the wettest period in mid spring, but otherwise distributed more or less evenly throughout the year. Mean daily maximum temperatures range from 27.5 °C in mid-summer to 14.2 °C in mid-winter, and mean daily minimum temperatures range from 12.4 °C in mid-summer to 2.4 °C in mid-winter. The *P. correctum* population occupies an area approximately 300 m by 20 m. The Munro rail reserve site has few weed species but a high pest animal population, consisting mainly of rabbits and hares.

2.3. Fire history

Over the past century the site was regularly burnt every 1–2 years in early summer for fuel reduction. The practice was abandoned in the early 1980s in favour of the use of chemical herbicides (Lunt, 1994). Similar burning practices were common along rail reserves throughout Victoria during this period, promoting treeless vegetation dominated by native grasses and herbs, which replaced the original forests and woodlands (Lunt, 1994, 1997). Many of these sites are now important repositories for the State's threatened grassland flora (Stuwe and Parsons, 1977; Scarlett and Parsons, 1993; McDougall and Kirkpatrick, 1994). Burning resumed in the early 1990s in response to ecological concerns that chemical control of plant biomass was detrimental to the indigenous flora.

During the orchid census period (1992–2003), different sections of the site were deliberately burnt in different years as part of site management. Typically, half the site was burnt in 1 year and the other half in the following year. All fires were lit in early autumn except in 1991, when the whole site was burnt in late winter/early spring, and in 1996 and 2003, when the whole site was burnt in early autumn.

2.4. Demographic census

A 350 m transect was placed through the longest axis of the orchid population in October 1992, and the location of each known plant was marked to within 15–25 cm with a short wooden stake at a distance perpendicular to the transect. Stainless steel pins were pushed into the ground 2 cm west of each plant to assist re-detection in later years. Each plant was assigned a set of co-ordinates (distance along the transect × distance to the plant in metres) and a unique number.

From 1992 to 2003, life state categories were recorded annually in October. These were: vegetative (leaf only), reproductive (flowering) or absent (non-appearance). Plants were assumed to be adults unless they were small (less than 10 cm high and 1 mm wide). In the first census year (1992) it was only possible to detect flowering plants, as vegetative plants consisting of a single narrow leaf were indistinguishable from many other monocotyledons. Thus, some plants were not recorded until they flowered in later years but all monitored plants were detected within 3 years from the start of the study. The census was repeated in October 2004; these data are not reported here, but were used to determine whether plants that did not appear in the last few years of the study were dormant or dead (see 'data analysis' below). From 1995 to 1998, plants were censused monthly from May to December and fortnightly during the flowering season (October). At each visit leaf length and width, flowering stem height, number of flowers and number of seed capsules on each plant were recorded. Leaf width measurements (measured in August when maximum annual width had been reached) continued until 2003.

From 1996 to 1998, vegetation biomass was sampled at 33 locations within the area of occupancy of the population. Samples were more or less evenly distributed across the site but avoided *P. correctum* plants. All standing vegetation was clipped to ground level in a 50 cm × 50 cm area, oven dried at 80 °C for 48 h and biomass calculated in grams per 0.25 sq m.

To assess grazing impacts, in 1996 open-topped, plastic mesh guards were placed around half the plants in the population to protect them from rabbits and hares. Guards were removed in December 1998 after plants died back to tubers.

The number of years since the most recent fire was recorded for each plant in October each year. Fires that occurred earlier in the year were designated as having occurred 0.5 years earlier.

Annual and monthly rainfall data from Stratford weather station (20 km south-west of the study site) were obtained from the Commonwealth Bureau of Meteorology, Melbourne except for 1995 and part of 1996 and 1997 when data were obtained from East Sale weather station, approximately 50 km south-east of the study site, owing to the absence of measurements from Stratford. A comparison of longterm monthly means indicated that the two rainfall stations experienced similar rainfall patterns and monthly totals. Rainfall was calculated for (i) the spring and summer prior to the flowering season (September–February), (ii) the autumn and winter

prior to the flowering season (March–August), and (iii) the 12 months immediately prior to the flowering season.

2.5. Data analysis

It was not always possible to accurately ascertain whether plants that did not appear in the final years of the census were dormant or dead. However, this information was needed to enable dormancy rates to be estimated to maintain sufficient data for analyses. Since the proportion of re-emerging plants declined significantly as the duration of dormancy increased (see Section 3), we arbitrarily assumed that all plants that did not emerge in both the final 3 (or more) years of the census plus the subsequent 2004 census were dead. By contrast, plants that did not emerge in the final 1–2 years of the census plus the subsequent year were deemed to be dormant. In practice, these rules applied to 30% of plants: 30 plants (24%) were assumed to have died and 6 plants (5%) were assumed to be dormant.

To determine whether the total number of plants emerging, sterile or flowering was cyclical we used spectral density plots (Fisher's Kappa test statistic, Fry, 1993). The null hypothesis was that the values in the series were drawn from a normal distribution with a variance of one, against the alternative that the series was cyclical with some periodic component. To determine whether the number of plants emerging, and in a vegetative or flowering state was dependent on some time lag (1–6 years), we used partial auto-correlation plots. This test describes the correlation between all the pairs of points in the time series with a given separation in time, or lag, using the Pearson product moment correlation coefficient (Fry, 1993). To determine whether mean leaf width of flowering and vegetative plants differed significantly we compared the maximum annual leaf width of all plants that emerged between 1995 and 1998 using the t-test (Quinn and Keogh, 2002).

The census data were allocated to two categories representing different fire intervals. Category 1 contained data for census years with fire intervals of <3 years, and category 2 contained data for those years with fire intervals of >3 years. These time intervals were chosen to approximate presumed optimal (category 1) or detrimental (category 2) fire regimes for maintaining structural and botanical values in comparable grasslands in south-eastern Australia (Lunt and Morgan, 2002). In addition, these also represented a change from 0.5 to 2.5 years fire intervals early in the census period to longer fire-free periods (3.5–6.5 years) near the end of the census. Average life state transition probabilities, sensitivities and elasticities (Caswell, 2001) were calculated for each life state (flowering, vegetative, dormant) until stable stage distribu-

tions were reached for both fire intervals and follow Tremblay and Hutchings (2003). Average transitions of each life state were compared between the two fire intervals.

Individual cross-correlation plots (time-lag 1–6 years) were used to evaluate if the number of flowering and vegetative plants, and the total number of emergent plants were correlated with: (i) spring/summer rainfall immediately prior to flowering, (ii) autumn/winter rainfall immediately prior to flowering, and (iii) total rainfall in the 12 months prior to flowering. The Pearson product moment correlation coefficient was used to examine relationships between biomass accumulation over time and time since fire, and biomass accumulation and rainfall (Quinn and Keogh, 2002). Generalised linear modelling with a logit link function (Quinn and Keogh, 2002) was used to test whether caging affected the number of plants that were grazed over time.

Data were log or square root transformed where necessary to satisfy assumptions associated with the analyses (Quinn and Keogh, 2002). In all cases $p < 0.05$ was used to reject the null hypothesis. Statistical packages used included Minitab Release 14 (Minitab® Inc.), GenStat 7th Edition (Lawes Agricultural Trust, 2004) and JMP (www.jmpdiscovery.com).
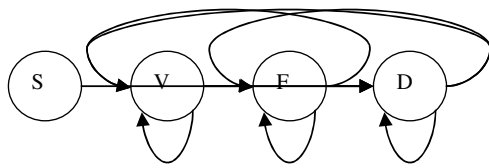
3. Results

3.1. Detection

Occasionally orchids were not detected owing to marker pegs being lost or damaged, or because the thick grass sward made detection difficult. In total, six plants were not re-detected (<0.1% of the total number of surveys), giving an overall detection rate >99.5%.

3.2. Population size and overall emergence

Over the 12-year period, 124 plants were recorded in the population, after a starting figure of 54 in 1992 (Table 1). All life history stages were observed over the census period (Fig. 1). The total number of emergent, vegetative and flowering plants was not correlated with the number of plants in previous years (lag time 1–6 years prior, partial auto-correlation analysis, all $p > 0.05$) and did not follow any cyclical pattern (total emergent plants, Fisher's Kappa test statistic = 2.10, $p = 0.56$; vegetative plants, Kappa = 1.99, $p = 0.63$; flowering plants, Kappa = 2.72, $p = 0.21$). The number of emergent plants (flowering + vegetative) varied greatly between years, from 1 plant in 2002 to 65 plants in 1998 (Table 1). In most cases (76% of emergence events) plants emerged for just 1 or 2 years before returning to dormancy in subsequent years. Only 24% of emergent events were for 3 or more years in a row (Table 2).

Table 1 – Numbers of flowering, vegetative and emergent tagged plants of *Prasophyllum correctum* at the Munro rail reserve, from 1992–2003

Year	1992	1993	1994	1995	1996	1997	1998	1999	2000	2001	2002	2003
Number of flowering plants	54	2	25	29	4	28	37	6	12	6	0	2
Number of vegetative plants	0	15	3	31	43	20	28	23	47	22	1	40
Number of emergent plants	54	17	28	60	47	48	65	29	59	28	1	42

Fig. 1 – Transitions between life cycle stages for *Prasophyllum correctum.* **S = seedling, V = sterile (vegetative), F = flowering, D = dormant.**

3.3. Recruitment and first detection

Five new plants of clonal origin, determined by excavation, were recorded during the census; four were flowering and one was sterile at first appearance. Five sterile seedlings were also recorded, designated as new recruits because of their low height and narrow leaf. Twelve sterile plants were detected that, judging from their size, were likely to be adults that went undetected in previous years. By contrast, 48 new flowering adult plants were recorded over the same period. It is possible that more seedlings and vegetative plants were present, but could not be readily distinguished since they are similar in morphology to many other monocotyledons.

3.4. Dormancy and mortality

In most cases (75% of dormancy events), plants were dormant for just 1 or 2 years before emerging in subsequent years, and only 25% of dormancy events were for 3, 4 or 5 consecutive years. In total, 44 plants (36% of the total recorded population of 124 plants) died during the 12-year monitoring period (Table 2); this includes 30 plants that did not emerge in the final 4 years (2001–2004). It is possible that some of these 30 plants may re-emerge in subsequent years, which may result in actual mortality having been slightly over-estimated.

3.5. Flowering

The number of flowering plants varied greatly, from 54 plants in 1992 to no plants in 2002 (Table 1). There was no significant correlation between the number of emerged plants and the proportion of emerged plants that flowered ($r = 0.28$, df = 1, $n = 20$, $p > 0.05$), which suggests that different processes control emergence and flowering. Almost all sequences of flowering events (81%) were of 1 year, and only 4% of sequences of flowering events extended over more than 3 consecutive years (Table 2).

3.6. Plant performance

Mean leaf width of flowering plants was greatest in 1996–1998 (3.1–3.9 mm) and declined in subsequent years. Similarly, the mean annual leaf width of non-flowering plants was greatest in 1996–1998 (1.2–1.7 mm) then declined from 1999 to 2003 (0.9–1.3 mm). Flowering plants were significantly larger than non-flowering plants in late winter (August) shortly preceding flowering ($t = -11.4$, df = 248, $p < 0.0001$). Mean leaf width of flowering plants in August was 3.0 mm (±0.1, $n = 69$) and for non-flowering plants, 1.5 mm (±0.06, $n = 181$). Mean flower stem height per annum ranged from 31 to 34 cm and the mean number of flowers per flowering plant ranged from 15 to 16. Average fruit set was 26% in the poor flowering year of 1996 but for the remaining years was 70–77%.

3.7. Fire regime and population dynamics

Time since fire ranged from 0.5 to 6.5 years. Shorter fire intervals (0.5–2.5 years) were most common and longer intervals (3.5–6.5 years) were rare (Table 3). The transition matrix dataset included 15 transitions (year to year) under short fire intervals (<3 years) and five transitions under long fire intervals (>3 years). Reproductive success in *P. correctum* was estimated as 0.0125, based on the number of new vegetative plants (adults + seedlings + clones) divided by the number of flowering plants over the census period. We only observed five seedlings but presumed that this was at least partly attributable to difficulty of detection. Thus, to calculate recruitment rate we included all new vegetative plants recorded each year. The same reproductive success rate was used in the short and long fire interval matrices to evaluate the effect of fire regimes on transitions and survivorship. Since we only observed 22 new vegetative plants throughout

Table 3 – Numbers of flowering, vegetative, dormant, and the total number of emergent *Prasophyllum correctum* plants recorded under short (<3 years) and long (>3 years) fire regimes at Munro rail reserve

Fire interval (years)	<3 years (n = 15)	>3 years (n = 5)
Number of flowering plants	190	14
Number of vegetative plants	198	66
Number of dormant plants	147	103
Total number of emergent plants	388	80

The number of times each fire interval occurred during the census period is shown in parentheses.

Table 2 – Frequency of consecutive years of emergence, dormancy and flowering for marked plants of *Prasophyllum correctum* between 1992 and 2003

No. of consecutive years	1	2	3	4	5	>5	Total
Number of emergence observations	112	42	11	18	11	9	203
Number of dormancy observations	96	80	21	29	10	30	266
Number of of flowering observations	134	25	0	3	4	0	166

Individual plants emerged, became dormant and flowered for different durations at different stages of the study.

the survey period, the recruitment rate is sufficiently small that any real differences between fire regimes are insignificant. We assumed that seedling dynamics were identical under both fire regimes and that all seedlings formed dormant plants in their first year.

Fire regimes affected transition probabilities and growth rate. The population growth rate under long fire intervals was 5% lower than under short fire intervals ($\lambda = 0.93$ vs. $\lambda = 0.98$). Under short fire intervals, 21% of reproductive plants remained reproductive in the following year, compared to only 15% under long fire intervals (Table 4). Similarly, 23% of vegetative plants became reproductive in the following year under short fire intervals, compared with only 2% under long fire intervals. Conversely, many more vegetative plants became dormant in the following year under long compared to short fire intervals (69% vs. 44%; Table 4). Most dormant plants remained dormant between time periods under both fire regimes although the proportion was higher under long fire intervals (75% vs. 60%). A far higher proportion of dormant plants moved to a reproductive state under short fire intervals (20% vs. 3%; Table 4). In summary, a larger fraction of individuals became or remained dormant when subjected to fire intervals exceeding 3 years.

Elasticity analysis showed that most of the proportional change in population growth rate would be affected by changes in the dormant stage. Changes in reproductive success, seedling recruitment and proportion of reproductive adults had little proportional effect on growth rates under either fire regime (Table 4). The expected stable stage distribution (Table 5) showed that seedling recruitment was expected to be rare under both fire regimes (<3%). The expected proportion of reproductive adults under long fire intervals was only 4% compared to 21% under short fire intervals. Most individuals (>50%) were expected to be dormant under both regimes (Table 5).

Table 5 – Expected stable stage distribution for *Prasophyllum correctum* based on census data 1992–2003		
Fire regime	<3 years	>3 years
Seedling	0.003	0.0004
Vegetative adults	0.251	0.185
Reproductive adults	0.214	0.036
Dormant	0.532	0.779

3.8. Rainfall

The study site experienced average or slightly above average annual rainfall in 1992, 1993, 1995 and 2001. However, the El Nino years of 1994 and 1997, which caused below average winter/spring rain throughout eastern Australia also affected the study site (Australian Bureau of Meteorology, 2004). Cross-correlations showed that total plant emergence was significantly negatively correlated with autumn/winter rain in the previous year ($r = -0.70$). There was no relationship between flowering and rainfall or between mean leaf width and rainfall.

3.9. Biomass

Based on data collected from 1996–1998, there was a significant positive correlation between biomass and time since fire ($r = 0.58$, df = 1, $p < 0.001$), and between biomass and spring/summer rain ($r = 0.79$, df = 1, $p < 0.001$), autumn/winter rain ($r = 0.76$, $p < 0.001$) and total rain in the previous 12 months ($r = 0.76$, df = 1, $p < 0.001$).

3.10. Response to grazing

Roughly equivalent numbers of plants emerged each year within and outside guards (Table 6), and there was no significant difference in mean leaf width between protected and

Table 4 – Stage based transition matrices comparing population dynamics under two fire regimes for *Prasophyllum correctum*, and corresponding elasticity matrices

Fire regime

<3 years ($n = 15$)   3 or more years ($n = 5$)

$$\begin{bmatrix} 0 & 0 & 0.0125 & 0 \\ 0 & 0.3259 & 0.3841 & 0.1543 \\ 0 & 0.2296 & 0.2134 & 0.2000 \\ 1 & 0.4444 & 0.4024 & 0.6029 \end{bmatrix} \qquad \begin{bmatrix} 0 & 0 & 0.0125 & 0 \\ 0 & 0.2874 & 0.375 & 0.1364 \\ 0 & 0.0230 & 0.15 & 0.0303 \\ 1 & 0.6897 & 0.475 & 0.7475 \end{bmatrix}$$

Corresponding elasticity matrices

$$\begin{bmatrix} 0 & 0 & 0.0027 & 0 \\ 0 & 0.0857 & 0.0861 & 0.0859 \\ 0 & 0.0613 & 0.0485 & 0.1130 \\ 0.0027 & 0.1107 & 0.0854 & 0.3180 \end{bmatrix} \qquad \begin{bmatrix} 0 & 0 & 0.0005 & 0 \\ 0 & 0.0615 & 0.0154 & 0.1230 \\ 0 & 0.0051 & 0.0064 & 0.0284 \\ 0.0005 & 0.1332 & 0.0176 & 0.6081 \end{bmatrix}$$

The four life states are: seedlings, vegetative adults, reproductive adults and dormant plants. The number of times a fire regime occurred during the census period is shown in parentheses.

Table 6 – Proportion of *Prasophyllum correctum* plants grazed within cages and outside cages, and the proportion of plants that flowered within and outside cages, 1996–1998			
Year	Emerged plants grazed in cages (*n*)	Emerged plants grazed outside cages (*n*)	Flowering plants in cages (*n*)	Flowering plants outside cage (*n*)
1996	0.16 (25)	0.57 (23)	0.12 (3)	0.04 (1)
1997	0.18 (22)	0.37 (27)	0.59 (13)	0.52 (14)
1998	0.12 (32)	0.18 (34)	0.63 (20)	0.5 (17)
No flowering plants were grazed over the 3-year period. *n* = total number of plants.			
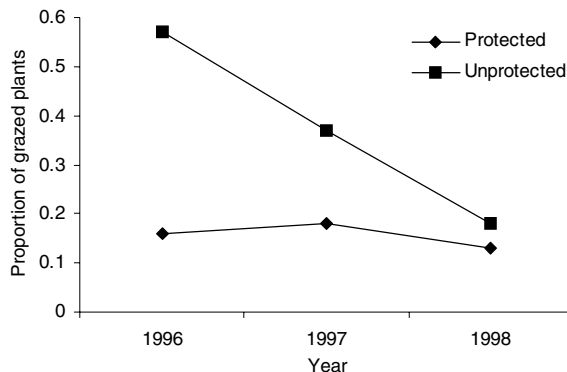
Fig. 2 – The proportion of grazed *P. correctum* plants protected by mesh guards, compared with the proportion of grazed, unprotected plants from 1996 to 1998 at the Munro rail reserve.

unprotected plants (*p* > 0.05). Protecting plants with guards had a significant effect on whether plants were grazed or un-grazed (*t* = −2.9, *p* = 0.004; Fig. 2). The effect was also significant over time (*t* = −2.61, *p* = 0.009; Fig. 2). Rabbits, hares and kangaroos were the most likely herbivores, although there was also some damage to plants from invertebrates. However, grazing impacts varied between years. In 1996 and 1997, guards provided significant protection against grazing (Table 6). Most grazing damage occurred in early winter, and affected newly emerged plants. By contrast, in 1998 there was little difference in the proportion of grazed plants inside and outside cages (Table 6). The number of flowering plants was higher within cages in the poor flowering year of 1996 when only 4 plants flowered in the entire population, but similar for the other 2 years (Table 6). Interestingly, flower spikes were not grazed at all in any single year, although some fruiting spikes were removed from unprotected plants in 1997 and 1998, possibly by birds.

4. Discussion

4.1. Variability in flowering and emergence

Results from this study demonstrate the high degree of annual variability in flowering and emergence of *P. correctum*, similar to that found in many long-term orchid studies (e.g. Tamm, 1972; Hutchings, 1987; Gregg, 1991; Light and MacConnaill, 1991; Falb and Leopold, 1993; Kindlmann and Balounová, 1999; Brzosko, 2002). Whilst fire regimes strongly

affected flowering and emergence, they did not account for the large annual variations observed. Since we found no direct relationships between flowering and past rainfall, a large proportion of the annual variation in flowering in this endangered orchid remains unexplained.

Rainfall has been found to contribute to orchid flowering patterns in many (Wells et al., 1998; Inghe and Tamm, 1988; Light and MacConnaill, 1991), but not all, studies (Falb and Leopold, 1993). The absence of observed rainfall influences in this study may reflect the use of relatively simple climatic indices, since only seasonal and annual rainfall over the previous 12 months was investigated. Phenological variations in orchids and other herbs are known to be influenced by other climatic factors, including temperature (Shefferson et al., 2001; Brzosko, 2002) and higher-order integrative weather indices (e.g. Lamb daily weather types; Dunnett et al., 1998), which were not investigated here.

Furthermore, past climatic influences may accumulate over time. Dunnett et al. (1998) and Herben et al. (1995) found that grassland community composition reflected climatic variations experienced over long time delays. Lagged climatic effects act through a variety of indirect mechanisms. For instance, weather variations may initially influence growth rates of dominant species, which then affect minor species in subsequent years (Dunnett et al., 1998). Similar interactions may occur in the *P. correctum* community, although their effects are likely to be difficult to detect owing to the complicating effects of frequent fires. Whilst we did not detect any direct influence of rainfall on flowering, plant emergence was inversely related to rainfall in the previous autumn and winter, and grassland biomass accumulation was positively associated with annual rainfall. These trends are consistent with the hypothesis that high rainfall may reduce *P. correctum* emergence indirectly by enhancing shoot competition from dominant grasses.

4.2. Dormancy patterns

Most dormancy periods for *P. correctum* were short: 75% were of 1 or 2 years duration. This is consistent with results from orchid studies in the northern hemisphere, which have found that dormancy periods most commonly range from 1 to 3 years (Hutchings, 1987; Waite and Farrell, 1998; Shefferson et al., 2001; Kéry and Gregg, 2004). For non-emergent orchids, the risk of mortality increases as the duration of dormancy extends (Wells, 1967; Tamm, 1972; Hutchings, 1987, 1989; Sieg and King, 1995). A number of studies have drawn attention to the difficulty of estimating the length of unobservable life stages (Gu and Swihart, 2003; Kéry et al., 2005). In this study,

dormancy could be accurately quantified for 50% of years. In the last 3 years of the census approximations were made for some individual plants based on the probability (0.75) of non-emergence after more than 3 years absence. Consequently, mortality may have been over-estimated during this period.

This may be significant, as this was also the period during which most plants experienced longer fire-free intervals (>3 years). Conversely, during the first 3 years of the census we are likely to have under-estimated dormancy. It was during this period that the population experienced more frequent fires (<3 years). Clearly these issues can only be resolved with an extended data set and excavation of plants, however the latter approach is not possible at this scale given the extreme rarity of the species.

4.3. Effect of fire intervals

Evaluation of elasticities under two different fire regimes showed that changes in the proportion of dormant plants remaining dormant in subsequent years made the highest contribution to changes in population growth rate. The proportional effect of dormancy under a fire regime of >3 years between fires was approximately twice as high as in the less frequent fire regime (60% cf. 32%). This suggests that the proportion of dormant plants in the population may be critical in determining population growth rates. Thus, the beneficial effect of frequent fires on *P. correctum* appears to be due to a reduction in dormancy levels (and possibly mortality levels) under a frequent burning regime.

Fire frequency also had an impact on flowering, with a higher proportion of plants moving to a reproductive state under shorter fire intervals (<3 years). Many terrestrial orchids are known to increase in abundance under management regimes including fire (Calder et al., 1989; Wheeler et al., 1998; Goldman and Orzell, 2000; Norton and De Lange, 2003), although the mechanisms causing elevated levels of emergence and flowering are not understood. Elevated soil nutrient levels immediately after fires may help to promote flowering, although levels of nutrient enrichment tend to be relatively insignificant after low intensity fires, at least in forests (Humphreys and Craig, 1981). No studies have been undertaken on post-fire soil nutrient levels in Australian grasslands (Lunt and Morgan, 2002). Most fires at Munro have been low intensity, as evidenced by patches of unburnt or partly burnt vegetation across the site. The effect of fire and the post-fire environment on orchid mycorrhizae is also unknown (Warcup, 1981). However, because *P. correctum* tubers are more than 3 cm below the soil surface (Coates, F., unpublished data), and soil heating during a fire is negligible below the immediate surface (Morgan, 1998), it is unlikely that mycorrhizal fungi are directly affected by grass fires.

Fire effects on *P. correctum* populations are likely to be caused indirectly, by altering the degree of shoot competition from dominant grasses. In productive grasslands, plant diversity and vigour is often maintained by disturbances that deplete the biomass of dominant grass species (Grime, 1973; Collins et al., 1999; Lunt and Morgan, 2002). An earlier study of the effects of fire frequency on post-fire flowering of grassland forbs at Munro revealed similar flowering responses in

other grassland forbs (Lunt, 1994); frequent fires promoted forb flowering and vigour, including flowering by another threatened orchid, *Diuris punctata* Sm. var. *punctata*. Progressive declines in flower abundance as time since fires increased were attributed to competition from dominant grasses that suppressed smaller associated forbs.

Few studies of orchid behaviour have compared orchid responses against other non-orchidaceous taxa. In a parallel 7-year study at the Munro site, annual variations in emergence and flowering of *P. correctum* were found to be strongly correlated with annual flower production by two common daisies (Lunt et al., 2005). This suggests that the factors promoting *P. correctum* flowering and emergence were not unique to this orchid, but were also experienced by other common forbs in the community.

4.4. Caveats

Life state transition analyses suggest that lambda values indicating population growth rates were <1 under both fire regimes (<3 years and >3 years). However, this negative estimate may be affected by under-estimation of recruitment levels because of the difficulty of detecting seedlings and over-estimating mortality of plants that had not re-appeared by the end of the census period. What is the true recruitment rate and death rate, and how long do tubers remain dormant before dying? Answering these questions is clearly a top priority for future research, notwithstanding practical difficulties associated with assessing these life history states.

These difficulties are not unique to this species. Orchid recruitment is known to be difficult to assess (Brzosko, 2002). New plants may remain as subterranean tubers for 1 or more years, and juvenile plants are often inconspicuous. Juvenile *P. correctum* plants produce only a single linear leaf, approximately 1 mm wide and <10 cm tall, which is difficult to find amongst thick grass. Detected plants were found by chance, usually in close proximity to tagged mature plants. Furthermore, the time between seed dispersal and development to the seedling stage may be extremely long in some species of orchids (>10 years, Wells, 1981; Willems, 1982), but little is known of seedling growth rates in Australian orchids in the wild (e.g., Batty et al., 2001). Given these difficulties, we believe that the estimated negative population growth rate should be treated cautiously and only used as an indicator of the relative growth rate between the two-fire regimes.

4.5. Management implications

These results have a number of implications for conservation management of this endangered species. Despite difficulties encountered in accurately assessing dormancy, it is clear that the population has not increased in number or expanded over the past decade. Instead, flowering and emergence have declined as fire frequency has declined. This decline was not associated with annual rainfall patterns. As we hypothesised, in situ conservation of *P. correctum* at Munro clearly depends on disturbance management, principally frequent fires, and to a lesser extent on controlling grazing of plants immediately after fires. Results suggest that maintenance of population

vigour requires frequent fires (<3 year intervals), and that intervals longer than this are likely to lead to extended dormancy, reduced flowering and possibly a decline in population growth rates. Frequent fires are unlikely to harm existing *P. correctum* plants if fires are lit in early autumn before plants emerge.

Fortunately, this frequent fire regime is unlikely to have adverse impacts on other plant species at the site (Lunt, 1994; Lunt and Morgan, 2002). In a previous study at the same site, Lunt (1994) suggested that frequent burning (every 2–3 years) was required to promote vigour of a range of forb species, including another threatened orchid, *Diuris punctata*. Other studies conducted in productive *Themeda*-dominated grasslands in south-eastern Australia suggest that plant diversity is promoted by frequent burning (Morgan, 1999; Morgan and Lunt, 1999; Lunt and Morgan, 2002), as is to be expected in productive grassland communities (Grime, 1973; Collins et al., 1999; Julita and Grace, 2002). Consequently, it appears that the disturbance regime that is required to promote orchid population growth is consistent with the requirements of the broader plant community.

Despite the enormous attention to orchid taxonomy and identification in Australia, this study provides some of the few data on plant responses to environmental factors measured over a number of years. We know of comparable long-term data collection for only three other orchids in Victoria: *Diuris dendrobioides* Fitzg., *D. punctata* Smith and *Thelymitra epipactoides* F. Muell. (Department of Sustainability and Environment and Parks Victoria, unpublished data). Clearly, more information on the responses of other threatened orchids is urgently required for the successful management of populations, particularly where ecological management using fire is concerned.

The results of this study have important implications for management of temperate grasslands in south-eastern Australia. A number of studies have demonstrated that the botanical values of important grassland reserves have declined as a result of non-implementation of planned disturbance regimes, especially burning (Scarlett and Parsons, 1982; Morgan, 1995; Lunt and Morgan, 2002). Similar outcomes have occurred in northern Europe and North America following the abandonment of traditional cultural practices (Stewart, 1992; Willems et al., 2001; Wotavová et al., 2004). Less than 0.01% of native grasslands now remain in Victoria and active management of these remnants is vital for the preservation of their herbaceous flora, including rare or threatened species.

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REFERENCES

Auld, T.D., O'Connell, M.A., 1991. Predicting patterns of post-fire germination in 35 eastern Australian Fabaceae. Australian Journal of Ecology 16, 53–70.

Australian Bureau of Meteorology, 2004. Rainfall Deficiencies Information. Australian Government Bureau of Meteorology http://www.bom.gov.au.

Backhouse, G.N., Cameron, D., 2005. Application of the IUCN 2001 Red List Categories for Determining the Conservation Status of the Native Orchids of Victoria, Australia. Selbyana 25 (2), in press.

Backhouse, G., Jeanes, J., 1995. The Orchids of Victoria. The Miegunyah Press, Carlton.

Barnett, J.M., 1984. The initial effects of fire on orchids in a stringybark-box forest. Victorian Naturalist 101, 188–190.

Batty, A.L., Dixon, K.W., Brundrett, M., Sivasithamparam, L., 2001. Constraints to symbiotic germination of terrestrial orchid seed in a mediterranean bushland. New Phytologist 152, 511–520.

Bowman, D.M.J.S., 1998. Tansley Review No. 101: The impact of Aboriginal landscape burning on the Australian biota. New Phytologist 140, 385–410.

Brzosko, E., 2002. Dynamics of island populations of *Cypripedium calceolus* in the Biebrza river valley (north-east Poland). Botanical Journal of the Linnaean Society 139, 67–77.

Burke, M.J.W., Grime, J.P., 1996. An experimental study of plant community invasibility. Ecology 77, 776–790.

Calder, D.M., Cropper, S.C., Tonkinson, D., 1989. The ecology of *Thelymitra epipactoides* F. Muell. (Orchidaceae) in Victoria, Australia, and the implications for management of the species. Australian Journal of Botany 37, 19–32.

Caswell, H., 2001. Matrix Population Models. Sinauer Associates, Inc., Sunderland, MA.

Coates, F., Lunt, I., Wapstra, H., 1999. Draft Recovery Plan – *Prasophyllum correctum* (Gaping leek orchid). School of Botany, La Trobe University, Vic..

Collins, S.L., Knapp, A.K., Briggs, J.M., Blair, J.M., Steinauer, E.M., 1999. Modulation of diversity by grazing and mowing in native tallgrass prairie. Science 280, 745–747.

Connell, J.H., 1978. Diversity in tropical rainforests and coral reefs. Science 199, 1302–1310.

Cropper, S.C., Calder, D.M., Tonkinson, D., 1989. *Thelymitra epipactoides* F. Muell. (Orchidaceae): the morphology, biology and conservation of an endangered species. Proceedings of the Royal Society of Victoria 101, 89–101.

Dunnett, N.P., Willis, A.J., Hunt, R., Grime, J.P., 1998. A 38-year study of relations between weather and vegetation dynamics in road verges near Bibury, Gloucestershire. Journal of Ecology 86, 610–623.

Falb, D.L., Leopold, D.J., 1993. Population dynamics of *Cypripedium candidum* Muhl. ex Willd., small white ladyslipper, in a western New York fen. Natural Areas Journal 13, 76–86.

Fry, J.C., 1993. Biological Data Analysis: A Practical Approach. Oxford University Press, Oxford.

Gill, A.M., 1981. Adaptive responses of Australian vascular plant species to fires. In: Gill, A.M., Groves, R.H., Noble, I.R. (Eds.), Fire and the Australian Biota. Australian Academy of Science, Canberra, pp. 243–272.

Goldman, D.H., Orzell, S.L., 2000. Morphological, geographical, and ecological reevaluation of *Calopogon multiflorus* (Orchidaceae). Lindleyana 15, 237–251.

Gregg, K.B., 1991. Variation on behaviour of four populations of the orchid *Cleistes divaricata*, an assessment using transition matrix models. In: Wells, T.C.E., Willems, J.H. (Eds.), Population Ecology of Terrestrial Orchids. SPB Academic Publishing, The Hague, The Netherlands, pp. 139–159.

Gregg, K.B., 2004. Recovery of showy lady's slippers *Cypripedium reginae* (Walter) from moderate and severe herbivory by white-tailed deer *Odocoileus virginianus* (Zimmerman). Natural Areas Journal 24, 232–241.

Grime, J.P., 1973. Competitive exclusion in herbaceous vegetation. Nature 242, 344–347.

Gu, W., Swihart, R.K., 2003. Absent or undetected?. Effects of non-detection of species occurrence on wildlife-habitat models. Biological Conservation 116, 195–203.

Herben, T., Krahulec, F., Hadincova, V., Pechackova, S., 1995. Climatic variability and grassland community composition over 10 years: separating effects on module biomass and number of modules. Functional Ecology 9, 767–773.

Humphreys, F.R., Craig, F.G., 1981. Effects of fire on soil chemical, structural and hydrological properties. In: Gill, A.M., Groves, R.H., Noble, I.R. (Eds.), Fire and the Australian Biota. Australian Academy of Science, Canberra, pp. 178–200.

Hutchings, M.J., 1987. The population biology of the early spider orchid, *Ophrys sphegodes* Mill. I.A demographic study from 1975 to 1984. Journal of Ecology 75, 711–727.

Hutchings, M., 1989. Population biology and conservation of *Ophrys sphegodes*. In: Pritchard, H.W. (Ed.), Modern Methods in Orchid Conservation. Cambridge University Press, Cambridge, pp. 101–115.

Hutchings, M.J., 1990. The role of demographic studies in plant conservation: the case of *Ophrys sphegodes* in chalk grassland. In: Hiller, S.H., Walton, D.W.H., Wells, D.A. (Eds.), Calcareous Grasslands – Ecology and Management, Proceedings of a Joint British Ecological Sociey/Nature Conservancy Council Symposium 14 – 16 September 1987 at the University of Sheffield. Bluntisham Books, Bluntisham, Huntingdon, pp. 106–111.

Hutchings, M.J., Mendoza, A., Havers, W., 1998. Demographic properties of an outlier population of *Orchis militaris* L. (Orchidaceae) in England. Botanical Journal of the Linnaean Society 126, 95–107.

Huynh, T., 1999. In Vitro Propagation of the Endangered Gaping Leek Orchid, *Prasophyllum correctum*. Honours Thesis, Royal Melbourne Institute of Technology University, Melbourne.

Inghe, O., Tamm, C.O., 1988. Survival and flowering of perennial herbs. V. patterns of flowering. Oikos 51, 203–219.

Jones, D.L., 1998. Native Orchids of Australia. Reed, Sydney.

Julita, H.M., Grace, J.B., 2002. Effects of disturbance on germination and seedling establishment in a coastal prairie grassland: a test of the competitive release hypothesis. Journal of Ecology 90, 291–302.

Keith, D.A., Williams, J.E., Woinarski, C.Z., 2002. Fire management and biodiversity conservation: key approaches and principles. In: Bradstock, R., Williams, J., Gill, A.M. (Eds.), Flammable Australia: The Fire Regimes and Biodiversity of a Continent. Cambridge University Press, Cambridge, pp. 401–425.

Kershaw, P.A., Clark, J.S., Gill, M., D'Costa, D.M., 2002. A history of fire in Australia. In: Bradstock, R., Williams, J., Gill, A.M. (Eds.), Flammable Australia: The Fire Regimes and Biodiversity of a Continent. Cambridge University Press, Cambridge, pp. 3–25.

Kéry, M., Gregg, K.B., 2003. Effects of life-state on detectability in a demographic study of the terrestrial orchid *Cleistes bifaria*. Journal of Ecology 91, 265–273.

Kéry, M., Gregg, K.B., 2004. Demographic analysis of dormancy and survival in the terrestrial orchid *Cypripedium reginae.* Journal of Ecology 92, 686–695.

Kéry, M., Gregg, K.B., Shaub, M., 2005. Demographic estimation methods for plants with unobservable life states. Oikos 108, 307–320.

Kindlmann, P., Balounová, Z., 1999. Flowering regimes of terrestrial orchids: unpredictability or regularity? Journal of Vegetation Science 10, 269–273.

Kull, T., 1995. Genet and ramet dynamics of *Cypripedium calceolus* in different habitats. Abstracta Botanica 19, 95–104.

Light, M.H.S., MacConnaill, M., 1991. Patterns of appearance in *Epipactis helleborine* (L.) Crantz. In: Wells, T.C.E., Willems, J.H. (Eds.), Population Ecology of Terrestrial Orchids. SPB Academic Publishing, The Hague, The Netherlands, pp. 77–87.

Lunt, I.D., 1994. Variation in flower production of nine grassland species with time since fire, and implications for grassland management and restoration. Pacific Conservation Biology 1, 359–366.

Lunt, I.D., 1997. Effects of long-term vegetation management on remnant grassy forests and anthropogenic native grasslands in south-eastern Australia. Biological Conservation 81, 287–297.

Lunt, I.D., Morgan, J.W., 2002. The role of fire regimes in temperate lowland grasslands of south-eastern Australia. In: Bradstock, R., Williams, J., Gill, A.M. (Eds.), Flammable Australia: The Fire Regimes and Biodiversity of a Continent. Cambridge University Press, Cambridge, pp. 177–196.

Lunt, I.D., Coates, F., Spooner, P., 2005. Grassland indicator species predict flowering of endangered Gaping Leek-orchid (*Prasophyllum correctum* D.L. Jones). Ecological Management and Restoration 6, 69–70.

McDougall, K., Kirkpatrick, J.B., 1994. Conservation of lowland native grasslands in South-eastern Australia. World Wide Fund for Nature Australia, Sydney.

Morgan, J.W., 1995. Ecological studies of the endangered *Rutidosis leptorrhynchoides*. 2. Patterns of seedling emergence and survival in a native grassland. Australian Journal of Botany 43, 13–24.

Morgan, J.W., 1998. Small-scale plant dynamics in *Themeda triandra* grasslands in south-eastern Australia. Journal of Vegetation Science 9, 347–360.

Morgan, J.W., 1999. Defining grassland fire events and the response of perennial plants to annual fire in temperate grasslands of south-eastern Australia. Plant Ecology 144, 127–144.

Morgan, J.W., Lunt, I.D., 1999. Effects of time-since-fire on the tussock dynamics of a dominant grass (*Themeda triandra*) in a temperate Australian grassland. Biological Conservation 88, 379–386.

Norton, D.A., De Lange, P.J., 2003. Fire and vegetation in a temperate peat bog: implications for the management of threatened species. Conservation Biology 17, 138–148.

Quinn, G.P., Keogh, M.J., 2002. Experimental Design and Data Analysis for Biologists. Cambridge University Press, Cambridge.

Scarlett, N.H., Parsons, R.F., 1982. Rare plants of the Victorian plains. In: Groves, R.H., Ride, W.D.L. (Eds.), Species at Risk: Research in Australia. Australian Academy of Science, Canberra, pp. 89–105.

Scarlett, N.H., Parsons, R.F., 1993. Rare or threatened plants in Victoria. In: Foreman, D.B., Walsh, N.G. (Eds.), Flora of Victoria. Introduction, vol. 1. Inkata Press, Melbourne, pp. 227–255.

Shefferson, R.P., Sandercock, B.K., Proper, J., Beissinger, S.R., 2001. Estimating dormancy and survival of a rare herbaceous perennial using mark-recapture models. Ecology 82, 145–156.

Sieg, C.H., King, R.M, 1995. Influence of environmental factors and preliminary demographic analyses of a threatened orchid, *Platanthera praeclara*. American Midland Naturalist 134, 307–323.

Stewart, J., 1992. The Conservation of European orchidsNature and Environment, vol. 57. Council of Europe Press, Strasbourg.

Stuwe, J., Parsons, R.F., 1977. *Themeda australis* grasslands on the Basalt Plains, Victoria: floristics and management effects. Australian Journal of Ecology 2, 467–476.

Tamm, C.O., 1972. Survival and flowering in some perennial herbs II. The behaviour of some orchids on permanent plots. Oikos 23, 23–28.

Thomas, P., Morris, C., Auld, T., 2003. Interactive effects of heat shock and smoke on germination of nine species forming soil seed banks within the Sydney region. Austral Ecology 28, 674–683.

Tremblay, R.L., Hutchings, M.J., 2003. Population dynamics in orchid conservation: a review of analytical methods based on the rare species *Lepanthes eltoroensis*. In: Dixon, K., Cribb, P., Kell, S., Barrett, R. (Eds.), Orchid Conservation. Kluwer Academic Press, Perth, Australia, pp. 183–204.

Waite, S., 1989. Predicting population trends in *Ophrys sphegodes* Mill. In: Pritchard, H.W. (Ed.), Modern Methods in Orchid Conservation. Cambridge University Press, Cambridge, pp. 117–126.

Waite, S., Farrell, L., 1998. Population biology of the rare military orchid (*Orchis militaris* L.) at an established site in Suffolk, England. Botanical Journal of the Linnaean Society 126, 109–121.

Waite, S., Hutchings, M.J., 1991. The effects of different management regimes on the population dynamics of *Ophrys sphegodes*: analysis and description using matrix models. In: Wells, T.C.E., Willems, J.H. (Eds.), Population Ecology of Terrestrial Orchids. SPB Academic Publishing, The Hague, The Netherlands, pp. 161–176.

Warcup, J.H., 1981. Effect of fire on the soil micro-flora and other non-vascular plants. In: Gill, A.M., Groves, R.H., Noble, I.R. (Eds.), Fire and the Australian Biota. Australian Academy of Science, Canberra, pp. 203–214.

Wells, T.C.E., 1967. Changes in a population of *Spiranthes spiralis* (L.) Chevall. at Knocking Hoe National Nature Reserve, Bedfordshire, 1962–1965. Journal of Ecology 55, 83–99.

Wells, T.C.E., 1981. Population ecology of terrestrial orchids. In: Synge, H. (Ed.), The Biological Aspects of Rare Plant Conservation. Wiley, Cambridge, pp. 281–295.

Wells, T.C.E., Cox, R., 1991. Demographic and biological studies of *Ophrys apifera*: some results from a 10 year study. In: Wells, T.C.E., Willems, J.H. (Eds.), Population Ecology of Terrestrial Orchids. SPB Academic Publishing, The Hague, The Netherlands, pp. 47–61.

Wells, T.C.E., Rothery, P., Cox, R., Bamford, S., 1998. Flowering dynamics of *Orchis morio* L. and *Herminium monorchis* (L.) R.Br. at two sites in eastern England. Botanical Journal of the Linnaean Society 126, 39–48.

Wheeler, B.D., Lambley, P.W., Geeson, J., 1998. *Liparis loeselii* (L.) Rich. in eastern England: constraints on distribution and population development. Botanical Journal of the Linnaean Society 141, 141–158.

Whelan, R.J., Rodgerson, L., Dickman, C.R., Sutherland, E.F., 2002. Critical life cycles of plants and animals: developing a process-based understanding of population changes in fire-prone landscapes. In: Bradstock, R., Williams, J., Gill, A.M. (Eds.), Flammable Australia: The Fire Regimes and Biodiversity of a Continent. Cambridge University Press, Cambridge, pp. 177–196.

Whigham, D.F., O'Neill, J., 1991. The dynamics of flowering and fruit production in two eastern North American terrestrial orchids, *Tipularia discolor* and *Liparis lilifolia*. In: Wells, T.C.E., Willems, J.H. (Eds.), Population Ecology of Terrestrial Orchids. SPB Academic Publishing, The Hague, The Netherlands, pp. 89–101.

Willems, J.H., 1982. Establishment and development of a population of *Orchis simia* Lamk. in the Netherlands, 1972–1981. New Phytologist 91, 757–765.

Willems, J.H., Melser, C., 1998. Population dynamics and life-history of *Coeloglossum viride* (L.) Hatm.: an endangered orchid species in the Netherlands. Botanical Journal of the Linnaean Society 126, 83–93.

Willems, J.H., Balounová, Z., Kindlmann, P., 2001. The effect of experimental shading on seed production and plant survival of *Spiranthes spiralis* (Orchidaceae). Lindleyana 16, 31–37.

Wotavová, K., Balounová, Z., Kindlmann, P., 2004. Factors effecting persistence of terrestrial orchids in wet meadows and implications for their conservation in a changing agricultural landscape. Biological Conservation 118, 271–279.