GEOPHYTES AS WEEDS: BRIDAL CREEPER (*ASPARAGUS ASPARAGOIDES*) AS A CASE STUDY

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Summary Geophytes are important weeds worldwide. Weedy geophytes can accumulate extensive underground reserves which enable them to crowd out native species and make their control extremely difficult. In southern Australia, many geophytes have been introduced as garden ornamentals and now invade a wide range of native plant communities. Bridal creeper can develop large tuber stores which are utilized for shoot emergence: high shoot densities and cover enable domination of the understorey. Shoots which emerge early in the growing season may flower while those emerging later remain vegetative. Fruit set can be high, but within established sites vegetative regeneration is probably more important. Management of bridal creeper, like other geophytes, requires techniques that both prevent the development of new storage organs and exhaust existing reserves.

INTRODUCTION

Geophytes are terrestrial plants which have perennating buds below ground. The above ground parts die back annually or in unfavourable conditions: regrowth is from reserves stored in subterranean organs such as bulbs, corms, tubers or rhizomes (Raunkiaer 1934).

Geophytic weeds have the potential to deleteriously affect native ecosystems. Accumulation of extensive storage reserves enables them to crowd out native species. In southern Australia, invasion of native ecosystems by geophytes has been viewed with increasing alarm (Humphries *et al.* 1991). Many species, especially those belonging to the Iridaceae and Liliaceae, were introduced into Australia from South Africa as garden ornamentals and are now environmental weeds (Parsons and Cuthbertson 1982, Humphries *et al.* 1991, Carr 1993).

Bridal creeper, *Asparagus asparagoides* (L.) W. Wight (Aparagaceae), a root tuber geophyte, is one of Australia's worst environmental weeds (Humphries *et al.* 1991). An understanding of its biology and ecology is essential for evaluating impacts on ecosystems as well as revealing any weak links which may be exploited by management techniques (Humphries *et al.* 1991, Briese 1993). I monitored several aspects of the growth and reproduction of bridal creeper to highlight why it is such a successful weed and to determine any vulnerable life-history stages that may be exploited by management practices.

MATERIALS AND METHODS

Field studies were conducted in mature *Leptospermum laevigatum* and *Leucopogon parviflorus* coastal scrub at Point Nepean National Park, Victoria. At Ti Tree Avenue (TT), where most detailed assessments of growth dynamics were made, a 32 × 15 m plot was established and divided into eight blocks, each containing one permanent 1 m^2 quadrat and sixteen 0.5 m^2 quadrats used to determine biomass. In both 1992 and 1993, no fruit set occurred within these quadrats. To better investigate flowering and fruiting phenology, in 1994 a 30 m transect was established within this plot as well as at two additional sites, Tasman Drive (TD) and Diamond Bay (DB), located 7 and 4.5 km from the original site, respectively.

Bridal creeper was well established at all three sites, forming a continuous cover which made it impossible to distinguish genets. Therefore, I collected data on a per ramet or a per unit area basis.

Shoot growth and survival The emergence and growth of bridal creeper shoots was monitored in the permanent quadrats at TT from April 1992 until February 1994. In 1992, cohorts of new shoots were tagged and counted every six weeks. The fate of five shoots per cohort was monitored through the growing season. The length and number of cladodes and flowers per shoot was recorded at each census date. Measurements of shoot length are likely to be conservative because many of longer shoots (>30 cm) appeared to suffer handling damage. To minimize this problem, in 1993 I recorded measurements on different shoots each time rather than on the same five shoots. To compensate for the increased number of shoots needed, these data were recorded less frequently (every 12 weeks). As in 1992, shoot emergence was monitored every six weeks.

Sexual reproduction Flowering and fruiting phenology of bridal creeper was monitored at all three sites so that any spatial variation in reproductive success could be determined. Along the 30 m transect at each site, 40 branchlets, each with at least five buds, were randomly selected and tagged. Each week from 21 July to 13 October 1994, I monitored the fate of five floral buds (randomly selected if the branchlet had more than five buds) by recording the numbers of buds, flowers and fruits. Reproductive success at each site was calculated from the percentage of buds which developed into fruits.

Fruit production was also determined at each site in 1994 by collecting above-ground material of bridal creeper within eight 0.5 m^2 quadrats randomly located along each 30 m transect. Collections were made on 22 October 1994 whilst fruits were still green to reduce losses to dispersers. I recorded the number of fruits and shoots as well as their dry weights after 7 days at 70°C.

Biomass The standing biomass of bridal creeper was determined at TT in 1992 and 1993 from eight 0.5 m^2 quadrats destructively sampled every six weeks. I recorded the percentage cover and density of shoots as well as the dry weights of shoot and root material. Roots were divided into new, mature and exhausted tubers. Tubers were not separated from rhizomes, except for isolated exhausted tubers. All future reference to tuber biomass also includes the mass of associated rhizomes. Shoots and tubers were dried at 70 and 95°C, respectively, until constant weight was achieved.

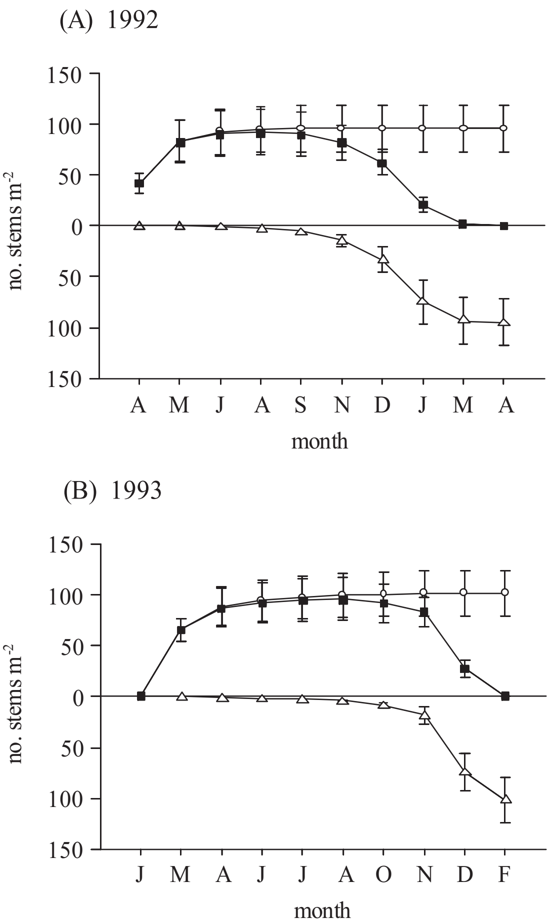

Figure 1. Cumulative recruitment (○) and senescence of shoot (△) and total shoot number (■) of bridal creeper at Point Nepean National Park, Victoria for shoots that emerged in (A) 1992 and (B) 1993. (±SE, N=8 quadrats).

RESULTS

Shoot growth and survival Most shoots of bridal creeper emerged early in the growing season (Figure 1). In 1992, shoots emerged rapidly in late March. After two weeks (early April), over 40% of all shoots had emerged and 80% had emerged by mid-May (eight weeks). In 1993, shoot emergence began much earlier in the season (late January) and 64% of all shoots emerged within five weeks. Shoot densities did not vary widely between years, reaching a maximum of 91.5 ± 22.4 (SE) shoots m^{-2} in August 1992 and 95.8 ± 21.2 shoots m^{-2} in August 1993.

Senescence of shoots during the growing season was low: in both years less than 20% had died by November. Most senescence was associated with the onset of warm weather. Of shoots emerging in 1992, most mortality (44%) occurred between December 1992 and January 1993. In 1993, senescence of shoots emerging was greatest between November and December when 54% of shoots died. Some 1992 shoots (20.4 ± 7.0 shoots m^{-2}) survived over the 1992–1993 summer when high levels of rainfall occurred (368 mm from November 1992 to January 1993). All of these shoots had senesced by April 1993. Thus, stem cohorts from 1992 and early 1993 overlapped, and green shoots of bridal creeper were continuously present from April 1992 until February 1994.

Early emergents of bridal creeper grew longer and produced more cladodes and flowers compared with later emergents, irrespective of year (Table 1). Comparing the maximum length and maximum number of cladodes for shoots in 1992 cohorts, shoots which emerged within approximately the first two weeks of the growing season (Cohort 1) were over three times longer, and had over five times as many cladodes than shoots in Cohort 2 (Table 1). In 1993, growth patterns of cohorts were similar to 1992.

Table 1. Average maximum shoot length and number of cladodes per shoot (SE) of the first three cohorts emerging from permanent quadrats in 1992. 'N' is the number of shoots followed per cohort.

Cohort	Length (cm)	No. cladodes
1 (N=40)	68.9 (8.5)	233.0 (40.7)
2 (N=40)	22.0 (4.8)	44.1 (10.1)
3 (N=37)	11.5 (2.8)	15.4 (4.7)

Sexual reproduction In both years at TT, only shoots from the first cohort developed floral buds. In 1992, an average of 4.7 ± 2.5 buds per shoot were produced in August. However, most had aborted by September and none remained by November. Similarly in 1993, 4.2 ± 2.0 buds and flowers per shoot were recorded in July, but all aborted by October. In both years, however, fruits were produced adjacent to the plot at TT (<10 m away).

In 1994, flowering of bridal creeper occurred at all three sites, lasting from 5 to 7 weeks. Fruit development commenced approximately three weeks after the initiation of flowering. The survivorship of floral structures varied among sites. The percentage of buds which flowered was slightly higher at DB (88.0 ± 2.9 %) than at both TT and TD (80.5 ± 4.7 and 80.5 ± 3.8 %, respectively). The percentage which actually matured into fruits, however, was 25 ± 4.5 % at DB, 20 ± 4.3 % at TD and only 3.5 ± 1.9 % at TT. A small proportion (£6%) of buds and flowers were attacked by insects: pooled across sites, only 4.3 % of these developed into fruits.

Fruit production also varied widely, both within and between sites. At TD, 1074.5 ± 460.5 fruits m^{-2} were produced. This was almost nine times the amount produced at DB (124.0 ± 59.9 fruits m^{-2}) and 75 times the amount produced at TT (14.3 ± 8.1 fruits m^{-2}).

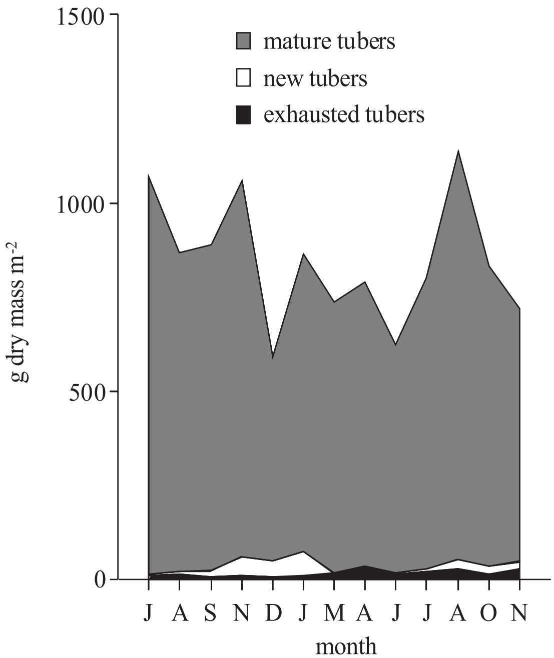

Figure 2. The average biomass (N=8 quadrats) of new, mature and exhausted tubers collected at six-week intervals from June 1992 to November 1993.

Biomass Seasonal dynamics of bridal creeper on destructively sampled quadrats were similar to those on permanent quadrats. Percentage cover, and above-ground biomass increased rapidly after initial emergence and remained high until shoot senescence began. Pooling results across the peak growing months of each year (May–November in 1992 and April–November in 1993), percentage cover averaged 70.8 ± 2.7 and 77.7 ± 1.6 % and above-ground biomass averaged 57.5 ± 5.2 and 75.8 ± 4.2 g dry mass m^{-2}.

Most of the biomass of bridal creeper was allocated to the root system. Allowing for the seasonal growth of shoots, at least 87% of the plant is found below ground. The rhizomes of bridal creeper entwined to form a continuous carpet-like layer just below the soil surface. Tuber biomass did not vary significantly across the sampling period, averaging 832 ± 38 g dry mass m^{-2} (P=0.24, ANOVA). Most of this consisted of viable, mature tubers, with new and exhausted tubers representing only a small proportion (Figure 2). New tubers were produced each year beginning in late-autumn: these comprised 65.8 ± 12.2 and 25.2 ± 7.4 g dry mass m^{-2} in 1992 and 1993, respectively. New tubers accounted for a maximum of only 8% of the total root biomass. The biomass of exhausted tubers did not vary significantly with time (P=0.33) and averaged 16.9 ± 2.0 g dry mass m^{-2}. This accounted for only 2% of total below-ground biomass.

DISCUSSION

In established sites, bridal creeper can reach very high densities and cover, enabling it to dominate the understory during the growing season. However, most of the plant biomass is actually found below ground. At Point Nepean, tuber reserves made up at least 87% of the plant's total biomass. Such a large store has several implications for plant growth.

Geophytes use stored reserves for shoot emergence and initial growth (Raunkiaer 1934, Mahoney 1982). At Point Nepean National Park, shoots of bridal creeper emerged *en masse* at the beginning of the season. These early emergents not only grew bigger than later emergents, but were also the only shoots that flowered.

Stored reserves may also buffer plant growth against unpredictable events (Dafni *et al.* 1981), including low rainfall (Boeken 1989) and herbivory. Bridal creeper shoots showed high survivorship, with only a small proportion senescing during the growing season. Over the study period, bridal creeper appeared to suffer little physiological stress and in both years the growing season even extended into summer. Herbivory was also negligible (K.L. Raymond unpublished data). Therefore, the use of stored reserves to supplement growth is probably minimal. In addition, neither above-ground biomass nor cover varied greatly during the season, suggesting that once shoots are fully developed, resources are directed towards storage.

Stored reserves should also buffer sexual reproduction. However, at my main site (TT), fruit set occurred in only one out of three years. The reasons for this variation in fruit production are unclear, but are likely to be caused by external factors rather than limited reserves. While high fruit production is possible, vegetative regeneration within established sites is likely to be more important.

The high biomass and cover of bridal creeper, both above and below ground, has serious implications for the biodiversity of native communities: competition for space, light and nutrients is likely to affect the regeneration of native species. Changes to the soil-litter environment may also affect soil micro-organisms and ecosystem processes such as litter decomposition and nutrient recycling. As a consequence, bridal creeper has the potential to modify both the structure and composition of the communities in which it occurs.

Bridal creeper appears to have few weak links in its life history, at least for the aspects investigated here. The accumulation of tuber reserves ensures its regeneration, either with or without sexual reproduction. The removal of early emerging shoots may be effective in reducing seed set and subsequent dispersal of bridal creeper to new sites. However, it is unclear what effect removal of early emergents will have on flowering of later cohorts and tuber production.

Although the reserves of geophytes are typically lowest following foliage development (Dafni *et al*. 1981, Mahoney 1982), the root biomass of bridal creeper did not vary significantly with time. This implies more than enough reserves had accumulated to compensate for the amount utilized for initial shoot emergence and growth. However, the infestation studied at Point Nepean is severe. In less dense stands, the use of stored reserves for shoot growth may have greater impact, simply because there are fewer tuber reserves. Similarly, genets of bridal creeper may also show changes in root biomass over time.

The storage reserves of other geophytic weeds also present problems for control, even if some degree of exhaustion occurs. Dormancy of organs (e.g. in *Hormeria flaccida*) and variation in timing of organ depletion (e.g. in *Oxalis pes-caprae*) reduce the effectiveness of control measures (Mahoney 1982, Parsons and Cuthbertson 1992).

Clearly, successful management of established infestations of bridal creeper, and other geopyhtes, will require techniques that both prevent the development of new storage organs and exhaust existing tuber reserves. This could be accomplished by the direct destruction of the storage organs or indirectly by repeated defoliation.

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