BALANCING CONSERVATION WITH COMMERCIAL USE:

AN EXPERIMENT TO GUIDE SUSTAINABLE EXPLOITATION

OF AN ECOLOGICALLY VULNERABLE KELP

by

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ABSTRACT

The Sea Palm, *Postelsia palmaeformis,* is an intertidal kelp of the Order
Laminariales, has a heteromorphic life history, and is endemic to the wave-
exposed rocky shorelines of the Northeast Pacific. *Postelsia* is also among the
most valued of seaweeds collected for the health- and wild-foods industry, and it
is collected commercially in Oregon and California. When collectors cut fronds
leaving the meristem intact they will regrow, allowing multiple collections per
season to be made from the same individuals. Commercial collection takes place
in California with minimal management or regulation, despite the fact that
Postelsia's life history characteristics make it especially vulnerable to
overexploitation. Though many California collectors advocate and use this
cutting method and maintain that it is sustainable, there is no scientific evidence
to support this claim. We experimentally mimicked the frond cutting method
used by commercial collectors and explored the effect of the frequency and
timing of collection on *Postelsia* survivorship, growth, and reproduction. Our
experiments were done in two areas of *Postelsia*'s biogeographic range: at the
southern range limit and near the center of its distribution. Results showed that
frond trimming has an immediate effect on *Postelsia*'s growth and reproductive
output, and though fronds trimmed early in the season are largely able to regrow
and eventually produce spores, they are somewhat delayed relative to untrimmed
plants. Timing of trimming was found to be more important than frequency,
because plants trimmed once late in the summer responded similarly to those
trimmed twice during the year. Variation between sites studied was limited to
general size and reproductive capabilities of plants; the effect of treatment was
essentially the same at both sites. Based on these results, we recommend that
commercial collectors take fronds, preserving the meristem, only once in the
spring. The findings of this study are ideal for consideration in the
implementation of an improved and appropriately designed management strategy,
balancing conservation with human exploitation.

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I. Introduction

The dramatic decline and decimation of species (Weber et al. 2000, Jackson et al. 2001, Doroff et al. 2003, Roman and Palumbi 2003, Schrope 2006) by fishing (Jackson et al. 2001, Myers and Worm 2003), whaling (Roman and Palumbi 2003, Springer et al. 2003, Baker and Clapham 2004), transportation, and waste management (Ruesink et al. 1995, Wonham et al. 2000, Jackson et al. 2001, Lodge et al. 2006, Nelson et al. 2006) is the legacy of centuries of human exploitation of marine ecosystems (Jackson et al. 2001, Lewison et al. 2004, Schrope 2006). The vast majority of marine ecosystems can no longer be assumed to be in a pristine state (Steneck and Carlton 2001), and pre-exploitation, fisheries-independent data for most commercially exploited species are almost non-existent (Dayton et al. 1998, Jackson et al. 2001, Mil-Homens et al. 2006), making restoration targets and plans for sustainable management difficult to define. Understanding the effects of commercial exploitation on natural populations is essential to ensure sustainable exploitation and conservation of natural resources (Lazo and Chapman 1996). Unfortunately, conservation and management research is often initiated well after the negative effects of exploitation become evident, and precautionary approaches can no longer be implemented.

Seaweeds, unlike whales or dolphins, are not inherently charismatic marine conservation targets, but many are considered foundation species (Dayton and Hessler 1972) that provide important ecosystem services including the provision of food and critical habitat for higher trophic levels. Seaweeds (defined here as multicellular photosynthetic protists), and kelps (Order Laminariales) in particular, have historically been and currently are used in many ways by humans. Kelps have been collected for

food and fertilizer for centuries in many places including Japan (Iida 1998), Chile

(Castilla and Bustamante 1989, Bustamante and Castilla 1990), and North America.

They were used for the production of alkali and potash in Ireland during the post-

medieval period (Forsythe 2006) and in California during World War I (Neushul 1989).

Kelps are collected to be used as feed in abalone farms (White et al. 1999, Rothman et al.

2006) and used for the extraction of alginates used in industrial processes (Lazo and

Chapman 1996, Tegner and Dayton 2000, Billot et al. 2003). Seaweeds are used in

animal feed, as food additives, in water purification systems, textile production,

pharmaceuticals and there is increasing interest in their use for production of biodiesel

(Doty et al. 1986). Seaweeds are also 'farmed' in areas where demand is high, such as

China (Tseng 1993, Feng et al. 2004), Spain (Martinez et al. 2006), Mexico (Munoz et al.

2004), and Canada (Thompson *personal observation*).

Despite the range of human uses and ecosystem services provided by seaweeds,

our understanding of the impacts of exploitation on their populations is limited (but see

(Bustamante and Castilla 1990, Ugarte et al. 2006)). To successfully manage

exploitation of seaweeds, we must address the same questions and problems that typically

arise in other fisheries, preferably before we suffer the symptoms of over-fishing that

currently afflict the vast majority of the world's fisheries (Safina 1994, Dayton 1998,

Myers and Worm 2003).

The Sea Palm, *Postelsia palmaeformis*, is an iconic seaweed of rocky shores, and

is also one of the most popular products collected and sold by commercial seaweed

businesses in western North America. *Postelsia* has an annual life history that is

ecologically vulnerable to overexploitation, and its commercial collection is virtually

unregulated in California where the majority of commercial collection occurs. In recognition of *Postelsia*'s susceptibilities, the majority of current commercial collectors have adopted what they believe are sustainable collection methods. However, at this time there have been no scientific studies conducted that verify that their collection methods are indeed sustainable.

We used an experiment to assess the impact on growth and reproduction of *Postelsia* by means of various collection methods currently used and recommended by commercial collectors as sustainable. This study follows-up on the first steps voluntarily adopted by commercial collectors, and provides experimental evidence to inform development of a scientifically sound management strategy for sustainable exploitation and conservation of this species, before it suffers the decline seen historically in many commercially exploited marine populations.

In this study, we examined the impact of different collecting methods in two parts of *Postelsia*'s range within California: southernmost and central range populations. We were especially interested in comparing the impacts of collecting methods recommended by Oregon scientists consulted by the Oregon Department of State Parks, with the findings of Kalvass (1994), as well as the collection methods recommended by one of the longest-operating seaweed businesses in California (Lewallen and Lewallen 1996). Scientists in Oregon proposed restricting collection to late in the summer, after *Postelsia* develop reproductive structures. This recommendation was made knowing that: 1) cutting individuals at the stipe is lethal, 2) some (but not all) commercial collectors use this method, and 3) method of take is not regulated. The scientists' recommendation with respect to timing of collection is especially important as some collectors specifically

market the younger, tender fronds as a higher-quality product. Thus, the recommendation of a late summer collection would yield a less desirable product. In contrast, Lewallen, realizing that the stipe cutting method was very destructive to local populations, recommended trimming fronds below the meristem (hereafter referred to as the frond trimming method) so they can regrow (and eventually produce spores (Kalvass 1994)), and further argued that multiple collections per season can be made without negative consequences (Lewallen and Lewallen 1996). Many commercial collectors in California appear to have adopted this method (Thompson *personal observation*). Although frond trimming seems to be preferable to the stipe-cutting method in that it is not lethal and fronds do regrow, and Kalvass (1994) suggested that allowing fronds to regrow would yield multiple collections and ensured spore production, we were suspicious that multiple collections could be made without negative effect to the local population due the potential energetic constraints on reproductive effort associated with an annual life history.

We are ultimately interested in population-level impacts of commercial collecting methods, but this study focuses first on describing the impact of different frequencies and timing of frond trimming on individual-level responses including growth, the timing of reproduction, spore production and spore viability. In addition, because species experience increased stress and become more rare at the edge of their ranges (Darwin 1859), we were also curious about the potential for variation in responses between center and southern edge populations. Furthermore, the central portion of *Postelsia's* range is in northern California where most of the commercial collecting currently occurs, thus this

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information will be especially relevant to developing regulations for this emerging

fishery. We specifically address the following questions in this study:

1. Does the impact of a single frond trimming differ if the trimming takes place prior
   to or after *Postelsia* have 'reproduced' (indicated by the presence of sorus tissue)?

2. Does the impact of frond trimming twice in the same year differ from trimming
   only once?

3. Does the answer to either of the above questions differ between center and
   southern edge populations?

II. Study Organism

   Postelsia is an intertidal kelp of the Order Laminariales found on wave-exposed

rocks (Dayton 1973), and is endemic to the west coast of North America, ranging from

Central California to British Columbia (Abbott and Hollenberg 1976). It has a

disturbance-mediated, annual life history with the heteromorphic, alternation of

generations life history characteristic of the Laminariales. Typically, macroscopic

sporophytes appear on the shore in late winter, sporophytes become reproductive in late

spring and summer, and senescing plants are largely removed from the rocks by the

following winter's storms (Dayton 1973, Paine 1979, 1988, Blanchette 1996).

Sporophytes produce flagellated zoospores on the sorus of each frond that drip down the

grooved fronds onto nearby surfaces, where they settle and grow into dioecious, haploid

gametophytes (Paine 1979). The gametophytes or possibly juvenile sporophytes persist

through the winter, often under the mussel bed, becoming apparent on the shore in early

spring, primarily in patches where the mussels and other biota have been disturbed by winter waves (Dayton 1973, Paine 1979, Blanchette 1996). *Postelsia* populations typically form 'groves' of upright sporophytes that form a canopy over other benthic organisms, much like a terrestrial forest, creating habitat for other species (Bertness et al. 1999). *Postelsia*, like many other intertidal kelps, offers shade and protection from desiccation for other intertidal organisms during periods of low tides (Dayton 1975, Bertness and Leonard 1997, Burnaford 2004). *Postelsia* can also be a source of localized disturbance as it can overgrow other organisms (Dayton 1973), increasing the drag forces imposed on them by waves, leading to their dislodgement and creating free space for other organisms to colonize (Dayton 1973).

Postelsia* has very specialized habitat requirements: it is typically found only on the most wave-exposed portions of rocky shores. These turbulent habitats, aside from assisting *Postelsia* by the winter removal of mussels, freeing substrate to be accessed by sporophytes (Blanchette 1996), also satisfy specific physiological requirements. *Postelsia* is restricted in its local distribution by environmental stresses associated with tidal height and wave exposure including desiccation and light limitation (Nielsen et al. 2006). *Postelsia* requires higher light levels than other kelps, growing at higher tidal elevations, and being sensitive to desiccation, benefits from the sea spray associated with these wavy shorelines (Nielsen et al. 2006). Furthermore, *Postelsia* has very limited dispersal and is therefore dependent on local reproductive success (Dayton 1973). Genetic analyses show relatedness of *Postelsia* individuals decreases as a function of distance between individuals (Coyer et al. 1997), and there is evidence of inbreeding (Kusumo et al. 2006). The genetic structure of *Postelsia* populations, including high

levels of homozygosity and small spatial scale genetic differentiation, reflect the localized scale of dispersal as well as the genetic bottlenecks that are created as populations go through 'boom-bust' cycles in natural abundance (Whitmer 2002). Although *Postelsia* does not typically disperse over large distances (with the exception of drifting plants) (Dayton 1973, Kusumo et al. 2006), studies on population persistence done in Washington by Paine (1988) experimentally demonstrate that a single reproductive individual is sufficient to 're-seed' a local population yielding an average of 21 individuals in the following year. However, the probability of local extinction doesn't fall below 0.5 until population size exceeds 91 individuals (Paine 1988). These results suggest that reducing survivorship or spore production has the potential to increase extinction probabilities and alter local population dynamics.

Regulations and Management

California Department of Fish and Game estimated that approximately 2-3 tons of *Postelsia* were collected in both 2000 and 2001 by four licensed collectors in Mendocino County (O'Brien and Miller 2004). There is only one commercial collector licensed in Oregon and there are none in Washington or British Columbia, comprising the remainder of *Postelsia*'s range. However, there are several additional individuals or small businesses that currently collect and sell *Postelsia* in northern California. *Postelsia* and other seaweeds can be found for sale in small packages and bulk bins in health food stores, food co-ops, and farmer's markets.

In California, existing regulations prohibit sport or recreational collection, and require special permission for scientific collection. However, commercial collection is

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permitted under kelp harvest/edible seaweed permit (fee = $100/year for California residents) (California Fish and Game Code section 6650-6657). There are no limits on the number of permits issued or amount of take allowed, and neither the method, timing, nor location of collection is mandated. The only places where commercial collection is explicitly prohibited by law are within state marine reserves and parks, however, there are only ~ 17 miles of coastline within California that have potential *Postelsia* habitat (exposed rocky coast) and fall under this special protection category. The permit holder must keep log books of total plant material collected but not necessarily broken down by species, however, a voluntary log of take by species is now requested of commercial licensees (Joann Eres, California Department of Fish and Game, Karina Nielsen *personal communication*). As a result of limited landings data, the impacts of commercial collection on species with particularly vulnerable life histories, such as *Postelsia*, remain effectively hidden from view.

Many commercial seaweed collectors recognize the potential vulnerability of this species, and as a result have made good faith efforts to use what they claim are sustainable methods. Commercial collectors also have informal agreements among themselves regarding traditional collecting territories (we intentionally use the term 'collect' instead of 'harvest' to distinguish between sowing and then harvesting a crop as in agriculture or silviculture, and collecting from wild populations, as the dynamics and impacts are distinct).

The current management of the Sea Palm market in California is in many ways typical of developing fisheries. Regulation of commercial collection is sorely lacking though scientific information on the basic life history and ecology of the species suggests

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that commercial take should be carefully managed, there is growing commercial interest in the product, and the collectors themselves are interested in managing the fishery sustainably. *Postelsia* currently balances on the edge where inadequate management could easily result in multiple localized population extinctions, or appropriate management could be implemented which would ensure sustainable use and conservation of this unique seaweed. Now is the time to develop and implement evidence-based management and regulation of this nascent "fishery".

III. Methods

Experimental Design

Our experiment was designed to test for impacts of different frond trimming frequencies and timing on *Postelsia* survivorship, growth, timing of reproduction, reproductive output and spore viability. The experiment was established in April 2006 and monitored through November 2006. We used two sites in California to test for potential geographic variation in the response of *Postelsia* populations to the different treatments associated with a theoretically predicted decline in ecological performance at a species range limit: Point Cabrillo (39° 20' 56" N, 123° 49' 40" W) in Mendocino County, and Piedras Blancas Point (35° 39' 55" N, 121° 17' 12" W) in San Luis Obispo County (Figure 1). Piedras Blancas Point (hereafter PB) is the last accessible population at the southern range limit for *Postelsia* while Point Cabrillo (hereafter PC) is located nearer to the center of *Postelsia*'s range. The true southernmost population during this study was at Disney Point, CA inside Pacific Gas and Electric Company's Diablo Canyon

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nuclear power plant property, but was too small and in a dangerous locale to support field experiments. PC was one of the few sites in Mendocino County where extensive commercial collection has not taken place in recent years, making it suitable for field collections.

We used a randomized block design with treatments applied to plots of individuals within the blocks. Four treatment levels were established to compare the impact of frond trimming at different frequencies and timing: 1) trim once in late spring (trim early); 2) trim once in late summer (trim late); 3) trim in late spring and again in late summer (trim twice); and 4) not trimmed (control). The trimming treatment mimicked the frond trimming method advocated by Kalvass (1994) and Lewallen (1996); all fronds on each plant were cut distal to the meristem, leaving ~ 2.5 cm to allow for regrowth. Trimming treatments were applied to all individuals within a plot, but measurements of response variables were made on sub-samples of individuals from each plot (see below for details). There were two replicates of each treatment level within each block and the experiment was replicated at the two study sites. Six blocks were established at PB and seven at PC (48 total plots at PB and 56 at PC). The 0.125-m^2 plots were marked at their corners with stainless steel washers stamped with plot numbers and affixed to the rock using a Bosch battery-powered hammer drill, stainless steel screws and plastic wall anchors. Blocks were haphazardly located in the middle portion of the intertidal range of each population thus avoiding potentially stressed individuals at all fringes of the population.

All plots were monitored prior to the first trimming and then 4-8 weeks thereafter over a period of 2-4 days depending on sea state and timing of low tides to investigate

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trimming effects. The experiment was established and the early trimming treatment

implemented in late April at PC and in mid-May at PB; both sites were subsequently

monitored in mid-late June and late July, when the late trimming treatment was

implemented immediately following the monitoring. PC was monitored again in early

September and early November. PB was monitored once more in early October.

Response Variables

We chose to monitor plant density as a proxy for survivorship instead of

monitoring survivorship of specific marked or mapped individuals due to the difficulty of

marking individual plants without damaging them, and the time-consuming nature of

mapping and relocating individuals. To assess frond growth after trimming we counted

frond density and then measured the length and width of three representative fronds from

sub-samples of five individuals per plot, all selected haphazardly but without

preconceived bias. The initial goal was to measure five individuals, but smaller samples

were taken when plot densities fell below five individuals due to natural mortality.

To quantify reproductive output we collected three fronds from each of three

plants per plot once sori were apparent. The fronds were returned to the lab for

measurements of sorus area, spore production and spore viability. Fronds were stored in

plastic bags in a cooler with ice for transportation to the lab, refrigerated in the dark

overnight and then processed the following day. In the lab, fronds were laid flat on a

light table with a ruler for scale, and a digital photograph was taken. The use of the light

table was to illuminate the frond from behind, making the sorus clearly visible. We used

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ImageJ image analysis software (Rasband 1997-2006) to measure frond and sorus areas from the digital photographs.

Spore production was estimated in the laboratory by inducing and then quantifying spore release. Following overnight storage in a dark refrigerator at 9°C degrees (Lewis 1995), we placed 1 cm^2 of sorus tissue in 0.95 mL of filtered seawater into a 1-dram glass vial. Vials were stored in a lit growth chamber at 12°C for 48 hours, the sorus tissue was removed and the samples were preserved with 0.05 mL of 37% formalin (Reed et al. 1997). We estimated the number of spores released per cm^2 of surface area by counting spores from two replicate aliquots of 10^{-4} mL preserved sample on a hemacytometer slide under a compound microscope at 400X magnification. The number of spores released per cm^2 over 48 hours was calculated using the average count x 10^4 x dilution factor. Average count refers to the average number of spores counted per 1 mm^2 area in the grid on the hemacytometer, and six 1-mm^2 areas on the hemacytometer were counted for each sample. The dilution factor for our sampling was 1, since no dilution was necessary for spore counting. To estimate the average number of spores released per plant over a 48-hour period we multiplied the average number of spores released per cm^2 of sorus of each plant by the average sorus area of the fronds, and then by the average frond density of each plant.

Spore viability was measured as the percent of released spores germinating after 24-48 hours. Germination was defined as the presence of a germ tube at least as long as the diameter of the spore (Reed et al. 1996). A 2-4 cm length of frond containing sorus tissue was cut from the center of the frond and placed on a microscope slide in a Petri dish with enough filtered seawater to cover. These dishes were then stored in a lit growth

chamber at 12°C for 24 hours. At 24 hours, the sorus tissue was removed, and the slide was examined for spores. Germinated and ungerminated spores were counted in five random fields of view on the slide at 400X using a compound microscope. After counting, the slides were replaced in the incubation chamber for an additional 24 hours and then recounted. Germination of *Postelsia* spores typically occurs within 24 hours (Lewis 1995). By waiting an additional 24 hours following the removal of the sorus tissue, we ensured that all spores released had at least 24 hours to germinate prior to sampling. We also estimated the number of viable spores produced per 0.125 m^2 per 48 hours by multiplying the number of spores produced per plant by the proportion of spores germinating and then by the density of plants in each plot.

Reproductive output was estimated in several ways: total sorus area of the plant, sorus area as a percent of total frond area, and area-specific spore release rate. In addition, we measured spore viability as the percentage of spores germinating after 48 hours. From these data we derived estimates of the average spore release rate per plant and by combining the latter with plant density, the number of viable spores released per m^2 within a 'Sea Palm grove.' We also evaluated whether or not sorus area was a good proxy for reproductive output (expressed as the plant-level spore release rate).

Statistical Analyses

To analyze the results of our experiment, which included both fixed and random effects, we used a generalized linear mixed model (Freund and Littell 1991). Site and treatment were analyzed as fixed factors, while block was random. Although the experiments were monitored over time, a repeated-measures approach to the statistical

analysis was not used for the following reasons: 1) different individuals within each plot were measured at each census date, 2) during the fall census dates, measurements were made during different months at the two study sites, and 3) as field time was often limited by sea state, we did not always measure all plots prior to the trim late treatment as plants in the trim early and trim twice treatments were identical then (had been trimmed once), as were plants in the trim late and control treatments (had not been trimmed). Data for all sub-sampled response variables were averaged up to the plot level prior to analysis. For the times when both sites were monitored within two weeks (or one low tide series) of each other we analyzed the data together, allowing us to assess site x treatment interactions. During sampling dates where there was a significant site x treatment interaction, we used a splice test (Freund and Littell 1991) to determine the nature of the interaction. The final censuses at the sites (two at PC and one at PB) occurred at least a month apart, so these data were analyzed separately for each month. Contrast statements testing *a priori* hypotheses were used when mathematically possible, otherwise we used the more conservative Tukey post-hoc multiple comparison test. Contrast statements were coded to test the following differences: 1) controls vs. trimmed (all three trimming treatment levels combined), 2) early vs. late trimming, 3) trimming once vs. twice, and 4) the interaction between number and timing of the trimmings. Data from the first census date were coded for all treatment levels, even though no trimming treatments had been applied, to ensure that there were no differences among the plots randomly assigned to the various treatment levels (i.e., non-significant trimming effects were expected). Transformations of the response variable data were made to improve the distribution of

the residuals if inspection of residual plots found severe violation of model assumptions and are indicated in Tables 1-8.

Analysis of covariance was used to assess the relationship between sorus area and spore release rates at the two sites, and to determine if the relationship differed between sites. The data over time were pooled as different individuals were measured over the course of the experiment, thus meeting the independence assumption of the statistical model. Both response variables were Log_{10} transformed to meet model assumptions, and data from a few individuals that were not releasing spores yet, but had a small amount of immature sorus tissue visible, were excluded from the analysis.

IV. Results

Plant density did not vary with trimming treatment at any time over the course of the study (Fig. 2, Table 1). However, densities did appear to decline somewhat more rapidly at PB than at PC through the late summer and into the fall (Fig. 2). Differences in growth among trimming treatments were evident in measurements of frond lengths and areas as well as in all metrics of reproductive output (see below). At the start of the study, both frond lengths and areas were indistinguishable between sites or among trimming treatments (Tables 2a and 3a). However, unmanipulated fronds were longer and had greater area at PC in all subsequent monitoring dates (Figs. 3 and 4, Tables 2b-f and 3b-f). In June, one month after the first trimming, trimmed fronds remained shorter than controls (Fig. 3, Table 2b) at both sites. When maximum frond length was achieved at both sites in July (Fig. 3), the effect of trimming remained evident (Table 2c), although fronds trimmed early approached control lengths (Fig. 3). Frond areas followed the same

trends as frond lengths, except that there was no evidence to suggest that the response to the treatments varied between sites (Table 3). By the fall there was no evidence of a difference in frond areas among treatments at PB, though in September at PC the effect of trimming was still quite clear (Fig. 4, Table 3d,e).

By September, the frond lengths of control and trim early plants at PC had converged, as did the frond lengths of the trim late and trim twice plants (Fig. 3). In the former case the convergence was most likely the result of 'catching up'; while in the latter case it clearly resulted from the lack of growth subsequent to the second trimming. Across both sites, fronds left untrimmed or trimmed early were substantially longer in the fall compared to fronds trimmed late in the summer (Fig. 3, Table 2d,e). Frond areas followed a similar trajectory, with strong differences evident among treatment levels in September at PC, but plants trimmed early still lagged behind control plants (Fig. 4, Table 3d). However, trimming effects were not evident later than September at either site (Fig. 4, Table 3e,f).

Although sori began to appear in late spring at both sites, sori were larger, sooner at PC both in absolute area and as a percentage of total frond area (Figs. 5 and 6, Tables 4a and 5a). Sorus areas of untrimmed fronds plateaued by July at PB, and by September at PC (Fig. 5). Trimming fronds resulted in decreased sorus area and percent sorus area after the first trimming at both sites through July, but the absolute amount of sorus area and the effect of trimming on sorus area remained greater at PC than at PB (Figs. 5 and 6, Tables 4b,c and 5b,c). After the second trimming at PC, sorus area of both the trim late and trim twice plants converged and remained lower than either trim early or untrimmed plants, and while trim early plants continued to increase their sorus area, they did not

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catch up with control plants (Fig. 5, Table 4d). By November at PC, the effects of the

trimmings were diminished, and sorus area was reduced overall (Fig. 5, Table 4f). At PB

in October, there was no evidence of a trimming effect on sorus area after the second

trimming (Fig. 5, Table 4e). Overall, these results from September and into the fall are

also reflected in proportion of sorus area (Fig. 6, Tables 5d-f). However, the proportion

of sorus area is maximized on the final census dates (Fig. 6, Table 5e,f) despite the

general loss of frond area (Fig. 4).

Spores were already beginning to be released by a few individuals during our first

sampling dates at each site in April and May (Fig. 7). Interestingly, spore release rates

were maximized and then sustained at both sites from July through the end of the study

period in November (Fig. 7). At the peak of spore production, individual plants release

billions of spores over a 48-hr period (Fig. 7). Early frond trimming resulted in a very

large decline in spore release in June at both sites (Fig. 7, Table 6b). The magnitude of

the effect weakened by July, but was still evident at both sites (Fig. 7, Table 6c). In

September, the plants at PC that had received the late trimming treatment (both the trim

late and trim twice treatments) released fewer spores (Fig. 7, Table 6d), and within that

group, plants trimmed twice released fewer spores than the plants that were trimmed late

only once. However, the plants at PC that were trimmed early in the season matched the

spore release rates of the untrimmed plants by September (Fig. 7). Thus, the effect of the

frequency of trimming on spore release rate depends on when the trimming is done (Fig.

7, Table 6d). By November however, the effects of trimming on spore release rates at PC

are largely dissipated (Fig. 7, Table 6f). By October at PB, no effect of trimming on

spore release rates was evident (Fig. 7, Table 6e).

Total sorus area is a good predictor of plant level spore release rates once plants are fully mature (Fig. 8), but the relationship varies geographically. The relationship between sorus area and spore release rate differed between sites (ANCOVA, sorus area x site interaction term (F= 4.792, p= 0.0296, df = 1, 237), thus individual regressions are presented for each site in Figure 8. Plants with total sorus areas less than 8.31 cm^2 tend to be immature, although this threshold size is somewhat larger at PC than at PB (Fig. 8, inset). Additionally, plants from PB release more spores for a given amount of sorus area than plants from PC (Fig. 8, see difference in slopes indicated in figure caption).

Although most plants did not have visible sori during our first sampling period at either site (Fig. 5), some individuals were already releasing spores (Fig. 7). Only a very small percentage of the spores released from either site on the first sampling date were able to germinate, but spores from PC were more likely to do so (approximately 5%; Fig. 9) than spores from PB (approximately 0.1 %; Fig. 9). The maximum germination success we observed in this study was 60-65% from untrimmed plants, but maximum germination success occurred earlier at PB (July), whereas the maximum for PC was in the fall (Fig. 9). There was no evidence of a difference in spore viability between trimmed and untrimmed plants in June or July at PB, or in July at PC (Fig. 9, Table 7b,c). However, there was some relatively weak evidence suggesting there may have been higher germination success at PB in July than at PC (Fig. 9, Table 7c). After the second trimming, and after maximum germination success was observed for both sites, there was strong evidence of a trimming effect in September and October for PC and PB, respectively (Fig. 9, Table 7d,e). Generally, plants trimmed twice or trimmed late had lower germination success than plants trimmed only once or not at all, though there was

an irregular response of trim twice plants at PC (Fig. 9). Additionally, a sustained

interval of high germination success (at least 50%) was maintained for a longer period of

time at PC than at PB, and there was no indication that either spore production or spore

viability was beginning to wane at PC by the November census period (Figs. 7 and 9).

To get a sense of how individual-level responses to frond trimming might

translate into population-level responses, we examined how the number of viable spores

released per unit area within Sea Palm groves varied over time and between sites (Fig.

10, Table 8). We found that during September, the unmanipulated group of the *Postelsia*

population at PC produced the highest number of viable spores per unit area (Fig. 10). In

June, when production of viable spores was low in both populations overall, the trimmed

populations at both sites produced fewer viable spores (Fig. 10). Graphically, this

difference in means appeared to persist through July at PB when spore viability was

maximized at this site, but not at PC (Fig. 10); however, the statistical evidence does not

support this interpretation (Table 8c). The most striking impact of trimming was evident

in September at PC, after the second trimming treatment was implemented (Fig. 10,

Table 8d). The number of viable spores produced at PC by the experimental populations

trimmed either once late in the summer or twice was substantially reduced compared to

those trimmed once early in the summer or not at all, strongly suggesting that the timing

of trimming has a greater impact than the frequency of trimming. At PB in October,

there was no statistical evidence of any effect of trimming (Table 8e), but the control

population produced a higher average number of viable spores when compared to any of

the trimmed populations (Fig. 10). By November at PC, evidence of a trimming effect

was gone (Fig. 10, Table 8f), and overall production of viable spores by the population had decreased dramatically (Fig. 10).

V. Discussion

The impact of frond trimming on *Postelsia* was evident in many different measures of growth and reproduction at some, but not necessarily all, times during this study. Typically, the strongest effects were evident one month after trimming and then declined substantially over the following two months. The timing of trimming tended to be more important than the frequency of trimming for some responses measured, though multiple trimmings were not without negative effects compared to the single late trimming treatment, for any response measured. Additionally, fronds trimmed late in the summer were less likely to recover than fronds trimmed earlier in the summer. These results are similar to the response of *Nereocystis luetkeana* (another kelp very closely related to *Postelsia*) in an experiment done to test its commercial collection in British Columbia. The results from this study showed that removing just the lamina, while preserving the meristem and basal portion of the laminae, reduced sorus production, canopy cover, percent of laminae with sorus, and lamina growth rate, but did not affect mortality of plants (Roland 1985), very like the results from our study on *Postelsia*. For those *Nereocystis* responses that experienced a reduction, the negative effect was more severe in plants where multiple collections were made than in plants where laminae were only taken once (Roland 1985).

The results from our study also showed evidence of geographic variation in *Postelsia*'s response to trimming treatments, as well as inherent geographic variation in the patterns of growth and reproduction in natural populations. Although in many cases we were able to clearly discern geographic differences, we must highlight an unavoidable limitation of our study that resulted from the reduced field time available in the fall months: our ability to resolve geographic differences in the fall was compromised because sampling of sites was staggered rather than simultaneous. The results suggest that even though the frond trimming method used by many conscientious commercial collectors is much more benign than the lethal stipe-cutting method used previously, it is not without consequence for growth and reproductive output of individuals. Below, I discuss these individual-level responses in more detail, interpret how these results might translate into population-level impacts, and close with recommendations for sustainable take from this wild population.

Growth and Reproduction

The growth metrics we focused on were frond lengths and areas as this is where the spore-producing sori will eventually develop, and the ultimate goal was to determine if the commercial collecting methods will impact local population dynamics. We knew from prior work (Kalvass 1994) that the frond (or blade) trimming method was not lethal, and that fronds trimmed once in May would regrow and eventually develop sorus tissue. We also knew that because the fronds regrow, commercial collectors believed this method allows them to make multiple collections per year from the same population without any negative impacts (Kalvass 1994, Lewallen and Lewallen 1996). However,

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this hypothesis had not been tested scientifically. Because *Postelsia* is an annual and appears to respond readily to annual variation in ocean conditions (Freidenberg 2002), we hypothesized that there would be energetic limitations on the number of times fronds could be collected and regrown without yielding negative consequences for reproductive output.

In this study, we observed that fronds trimmed early in the summer readily regrew, but that fronds trimmed late in the summer, after the appearance of mature sorus tissue, did not (Figs. 3 and 4). Additionally, frond length and total area were maximized by July at both sites and then declined rapidly thereafter, suggesting that senescence and loss of tissue to abrasion occurs in association with increasing wave action in the fall (Figs. 3 and 4). We thus suspect that once *Postelsia* shifts energy allocation toward reproduction and the development of sorus, it is less able to allocate energy to growth. Our observations of how *Postelsia* regrew in the field are consistent with this line of reasoning. We hypothesized that the fronds could either regrow and then develop sorus as they do over their natural growth cycle, or they could regrow vegetative and reproductive tissue simultaneously. We observed both phenomena: the former when fronds were clipped in late spring and the latter when fronds were clipped in late summer. Thus fronds trimmed before sorus production was fully underway apparently prioritized growth before allocating energy to producing reproductive structures, gaining their size back before spore production. The major potential ecological cost of this strategy is the delay in spore production compared to regrowing both vegetative and reproductive tissues simultaneously (Fig. 7). Furthermore, observations and measurements of *Postelsia* in 2007 showed that plants in northern California produced sorus tissue later in

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the season than in the year of this study (unpublished data). Results from our study have

shown that recovery is linked to the amount of time sorus has to regrow following

trimming (i.e. fronds trimmed late have less time to regrow). Thus, the later production

of sorus observed in 2007 could mean decreased recovery to late trimming in terms of

spore production. These differences in the way fronds regrow means there may be very

different consequences to using the same collection method at different times of year;

differences that may be key when considering best practices for managing commercial

activities.

Despite considerable study of the role of disturbance in mediating *Postelsia*'s life

history, and a general understanding of when sori begin to appear, no studies that we are

aware of document the period over which spores are shed, if spores are equally viable

over the period when they are shed, or if there is any geographic variation in the timing of

reproduction or reproductive output. Indeed, no studies on *Postelsia* as of yet

simultaneously examine populations from more than one geographic area. In this study

we saw striking patterns of geographic variation in several aspects of reproductive

activity, in addition to treatment effects that also varied geographically. Sori appeared

sooner and were larger in total area at the northern site (PC) than the southern site (PB)

(Fig. 5, Table 4). However, the number of spores released per plant was approximately

equivalent (Fig. 7, Table 6) because the population at PB was releasing more spores per

unit sorus area than the plants at PC (Fig. 7). But there is another layer to consider:

germination success over time was very different between the two populations (Fig. 9,

Table 7).   At PB germination success peaked in July and then fell in October, while at

PC germination success didn't peak until September and then remained relatively stable

until November (Fig. 9). The natural environment of a *Postelsia* spore is obviously different than the lab setting. However, though we measured spore release and germination success in the lab, we do not believe that having done so compromised our abilities to test the differences between trimming treatments or study sites.

When the various responses are integrated up to the population level and we estimate the number of viable spores produced per unit area, the differences in reproductive output between sites and treatments is evident (Fig. 10, Table 8). Output of viable spores over time appears to be more temporally constrained at PC than PB, with a clear peak occurring in September (Fig. 10). Knowing what time of year the majority of viable spores are shed should be an important consideration when determining the best way to manage the commercial take of this species.

Trimming fronds also impacted the reproductive output variables we considered, and these effects were not consistent between sites. There were clear negative impacts of trimming on sorus area and spore release rates that remained evident through September, were more striking at PC than PB, but then largely disappeared in the fall months at both sites (Figs. 5 and 7, Tables 4 and 6). In contrast, germination success was essentially the same across treatments until September when it became clear that trimmed fronds, especially those trimmed late in the summer, had lower germination success (Fig. 9, Table 7). When viewing the combined response at the population level in terms of number of spores produced per unit area we see what is potentially the most ecologically significant result from this experiment: populations trimmed late in the summer at PC produced ~ 95% fewer viable spores than those not trimmed or trimmed only once during the spring (Fig. 10). The impact of frond trimming at PB was not as striking, nor was it

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statistically significant, but the trend among the means was similar to what we observed at PC.

Temporally, we found some impacts of frond trimming to be consistent over a two-year period. We conducted a smaller experiment at Point Cabrillo in 2005 where *Postelsia* fronds were trimmed once in May, leaving the meristem intact. Frond length and sorus area measured in August and September, respectively, yielded similar results to our findings from 2006: untrimmed fronds were longer (31.01 +/- 2.24 (95% CI) cm) than trimmed fronds (22.71 +/- 8.12 (95% CI) cm), and had a larger sorus area (60.77 +/- 12.69 (95% CI) cm^2) than trimmed fronds (29.99 +/- 12.34 (95% CI) cm^2).

Other seaweed species are commercially exploited for food, food additives, and industrial processes, but few studies have formally investigated the impacts of exploitation on these populations (Bustamante and Castilla 1990, Ugarte et al. 2006). Generalities in the responses to exploitation seem to occur among species that share life history characteristics, as illustrated above between *Postelsia* and *Nereocystis*. Thus, although *Macrocystis pyrifera* is ecologically similar to *Nereocystis* since both species are functionally important as the makers of nearshore kelp forests, its response to commercial collecting is remarkably different (Springer et al. 2006). *Macrocystis,* in contrast to the annuals *Postelsia* and *Nereocystis*, is a large perennial that suffers no known negative effect of the collection; collectors take only vegetative portions of the plant and a small percentage of the plant's total biomass (Mackey 2006). Collected seaweeds of the Order Fucales, which have no free-living haploid phases unlike members of the Order Laminariales (including *Nereocystis*, *Macrocystis* and *Postelsia*), are affected much differently by human collection. For example, the major impacts on

populations of the commercially exploited perennials *Durvillaea antarctica* (Chile) and

Ascophyllum nodosum (north Atlantic coast of North America) are: 1) reduction of

abundance and biomass in *Durvillaea* populations (Castilla and Bustamante 1989), 2)

reduction in biomass of *Ascophyllum* (Lazo and Chapman 1996, Ugarte et al. 2006), but

no impact on growth or reproduction (Lazo and Chapman 1996). Clearly, commercial

collection of seaweeds has some ecological consequences. However, it is crucial to note

that the type and severity of impacts varies greatly depending on life history, collection

methods, and the intensity and frequency of collection. Successful management schemes

will need to account for species life histories, and evaluate population responses in light

of the magnitude and methods employed by commercial collectors.

Conservation and Management Recommendations

        Meeting conservation and commercial goals simultaneously when trying to

manage natural populations can often seem to be an impossible task. Often the

opportunity to adopt a precautionary approach has long been lost, and conservation

efforts are pitted against the vested economic interests of those whose livelihoods now

depend on overexploited wild populations. Adopting a precautionary approach can be

equally challenging for more banal reasons: there is no crisis now so why devote

resources to acquire the information and develop a management plan at this time?

However, viewed from a historical perspective, where "boom and bust" cycles and serial

depletion are seen repeatedly in so many commercially exploited marine populations, it

seems that a more appropriate question might be: if not now, when? By being proactive

instead of reactive perhaps conservation biology can be transformed from what Michael

Soulé (1985) called a 'crisis discipline' into one that instead supports economically and ecologically sustainable use of natural resources. The results of this proactive study of a developing "fishery" incorporated information from commercial collectors, with field experiments, and yielded results that can be used to guide sustainable commercial use of this natural population. Interestingly though, the data suggest the best approach is a compromise between the different views previously put on the table by scientists and collectors. Scientists in Oregon had recommended delaying collecting until after *Postelsia* develop sori to minimize the potential for negative population impacts, while collectors prefer collecting *Postelsia* before the sori develop, when the fronds are more delicate and tender. Collectors also believe that because fronds regrow when trimmed in late spring, two or more collections in one season could be made without negative impact. Based on our experiment that shows a huge negative impact on the number of viable spores being produced when fronds are trimmed in late summer, we instead recommend that fronds be trimmed distal to the meristem only once in late spring or early summer. This recommendation will yield a desirable product for collectors, and reduces the potential for negative effects on recruitment in the following year. This would also be relatively easy to implement and enforce by creating a *Postelsia* 'season.' Admittedly, this remains a precautionary recommendation because we have not yet demonstrated that decreased production of viable spores actually translates into decreased recruitment, and we are recommending a limit on take. However, this is the objective of an ongoing experiment that will be duly reported, and history has shown us that the collapse of a targeted species often occurs while management is designed to optimize take (Dayton 1998).

VI. Conclusions

The developing *Postelsia* "fishery" has the potential to be either a good model for how to balance conservation and commercial goals while exploiting a natural population or it can become the poster child for everything we do wrong with natural resource management. Our experiment has shown that the frond trimming method developed and used by many commercial collectors in California is best used in late spring or early summer, before *Postelsia* have developed sori. This allows the fronds to regrow and produce viable spores at similar rates and over the same time period as plants that were not clipped. Trimming fronds late in the summer is not recommended as it results in a sharp decrease in the production of viable spores. Although we did see evidence of differences between southern and northern population responses, the trends were similar, thus our recommendations are the same for both regions.

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Tables

Table 1. Results from mixed model ANOVA of *Postelsia* plant density.

	Num df	Den df	F	p-value
A. Spring (late April / mid May)				
Site (PC vs. PB)	1	11	2.77	0.1245
Treatment (Control vs. Trim Early)	3	24	1.53	0.2321
Site x Treatment	2	24	3.89	0.0343
Slice				
Treatment PC	2	24	0.58	0.5652
Treatment PB	3	24	3.20	0.0415
B. June				
Site (PC vs. PB)	1	11	0.68	0.4264
Treatment (Control vs. Trim Early)	1	11	0.34	0.5740
Site x Treatment	1	11	0.11	0.7512
C. July				
Site (PC vs. PB)	1	10	0.97	0.3468
Treatment (Control vs. Trim Early)	1	10	0.38	0.5493
Site x Treatment	1	10	0.10	0.7603
D. September (PC only)				
Treatment (all four)	3	18	0.54	0.6581
Contrasts:				
Control vs. Trimmed (trim early, trim late, and trim twice)	1	18	0.42	0.5254
Timing (trim early vs. trim late)	1	18	0.21	0.6526
Frequency (trim early and trim late vs. trim twice)	1	18	1.03	0.3244
Frequency x Timing (trim early vs. trim twice and trim late vs. trim twice)	2	18	0.62	0.5501
E. October (PB only)				
Treatment (all four)	3	15	0.06	0.9777
Contrasts:				
Control vs. Trimmed (trim early, trim late, and trim twice)	1	15	0.04	0.8484
Timing (trim early vs. trim late)	1	15	0.13	0.7247
Frequency (trim early and trim late vs. trim twice)	1	15	0.03	0.8648
Frequency x Timing (trim early vs. trim twice and trim late vs. trim twice)	2	15	0.08	0.9250
F. November (PC only)				
Treatment (all four)	3	18	0.15	0.9264
Contrasts:				
Control vs. Trimmed (trim early, trim late, and trim twice)	1	18	0.20	0.6567
Timing (trim early vs. trim late)	1	18	0.13	0.7260
Frequency (trim early and trim late vs. trim twice)	1	18	0.13	0.7251
Frequency x Timing (trim early vs. trim twice and trim late vs. trim twice)	2	18	0.13	0.8827

Note: Data for this response variable were square root transformed. In all analyses, all four treatments (see Methods section for details of trimming treatments) are coded in Spring to determine if differences exist among plots randomly assigned to the treatments prior to treatment, and in September, October and November after all treatments were applied to assess treatment effects. However, in June and July plots sampled were coded as either control (controls and trim late plots) or trim early (trim early and trim twice plots) as only the trim early treatment had been applied.

Table 2. Results from mixed model ANOVA of *Postelsia* frond length.

	Num df	Den df	F	p-value
A. Spring (late April / mid May)				
Site (PC vs. PB)	1	11	0.02	0.9005
Treatment (Control vs. Trim Early)	3	21	0.31	0.8164
Site x Treatment	2	21	1.35	0.2801
B. June				
Site (PC vs. PB)	1	11	69.90	<.0001
Treatment (Control vs. Trim Early)	1	11	252.06	<.0001
Site x Treatment	1	11	8.49	0.0141
Slice				
Treatment PC	1	11	90.03	<.0001
Treatment PB	1	11	165.48	<.0001
C. July				
Site (PC vs. PB)	1	11	112.25	<.0001
Treatment (Control vs. Trim Early)	1	11	16.32	0.0019
Site x Treatment	1	11	4.15	0.0665
D. September (PC only)				
Treatment (all four)	3	18	62.15	<.0001
Contrasts:				
Control vs. Trimmed (trim early, trim late, and trim twice)	1	18	75.09	<.0001
Timing (trim early vs. trim late)	1	18	91.80	<.0001
Frequency (trim early and trim late vs. trim twice)	1	18	20.37	0.0003
Frequency x Timing (trim early vs. trim twice and trim late vs. trim twice)	2	18	54.79	<.0001
E. October (PB only)				
Treatment (all four)	3	11	25.33	<.0001
Contrasts:				
Control vs. Trimmed (trim early, trim late, and trim twice)	1	11	38.33	<.0001
Timing (trim early vs. trim late)	1	11	37.17	<.0001
Frequency (trim early and trim late vs. trim twice)	1	11	2.61	0.1345
Frequency x Timing (trim early vs. trim twice and trim late vs. trim twice)	2	11	20.40	0.0002
F. November (PC only)				
Treatment (all four)	3	11	3.65	0.0478
Contrasts:				
Control vs. Trimmed (trim early, trim late, and trim twice)	1	11	0.65	0.4365
Timing (trim early vs. trim late)	1	11	10.10	0.0088
Frequency (trim early and trim late vs. trim twice)	1	11	0.80	0.3913
Frequency x Timing (trim early vs. trim twice and trim late vs. trim twice)	2	11	5.24	0.0252

Note: Data for this response variable were Log_{10} transformed. Refer to Table 1 for analysis details.

Table 3. Results from mixed model ANOVA of *Postelsia* frond area.

	Num df	Den df	F	p-value
A. Spring (late April / mid May)				
Site (PC vs. PB)	1	11	0.25	0.6248
Treatment (Control vs. Trim Early)	3	22	1.73	0.1901
Site x Treatment	2	22	3.30	0.0558
B. June				
Site (PC vs. PB)	1	11	25.43	0.0004
Treatment (Control vs. Trim Early)	1	11	99.50	<.0001
Site x Treatment	1	11	0.00	0.9577
C. July				
Site (PC vs. PB)	1	11	54.24	<.0001
Treatment (Control vs. Trim Early)	1	11	14.25	0.0031
Site x Treatment	1	11	0.00	0.9979
D. September (PC only)				
Treatment (all four)	3	18	26.16	<.0001
Contrasts:				
Control vs. Trimmed (trim early, trim late, and trim twice)	1	18	58.41	<.0001
Timing (trim early vs. trim late)	1	18	17.85	0.0005
Frequency (trim early and trim late vs. trim twice)	1	18	3.06	0.0970
Frequency x Timing (trim early vs. trim twice and trim late vs. trim twice)	2	18	10.52	0.0009
E. October (PB only)				
Treatment (all four)	3	12	2.96	0.0753
Contrasts:				
Control vs. Trimmed (trim early, trim late, and trim twice)	1	12	5.38	0.0389
Timing (trim early vs. trim late)	1	12	0.64	0.4385
Frequency (trim early and trim late vs. trim twice)	1	12	2.73	0.1246
Frequency x Timing (trim early vs. trim twice and trim late vs. trim twice)	2	12	1.56	0.2506
F. November (PC only)				
Treatment (all four)	3	15	0.37	0.7776
Contrasts:				
Control vs. Trimmed (trim early, trim late, and trim twice)	1	15	0.62	0.4423
Timing (trim early vs. trim late)	1	15	0.52	0.4818
Frequency (trim early and trim late vs. trim twice)	1	15	0.00	0.9760
Frequency x Timing (trim early vs. trim twice and trim late vs. trim twice)	2	15	0.26	0.7743

Note: Data for this response variable were Log_{10} transformed. Refer to Table 1 for analysis details.

Table 4. Results from mixed model ANOVA of *Postelsia* sorus area.

	Num df	Den df	F	p-value
A. Spring (late April / mid May)				
Site (PC vs. PB)	1	11	9.77	0.0097
Treatment (Control vs. Trim Early)	3	22	0.90	0.4581
Site x Treatment	2	22	2.03	0.1549
B. June				
Site (PC vs. PB)	1	11	3.56	0.0858
Treatment (Control vs. Trim Early)	1	11	63.04	<.0001
Site x Treatment	1	11	1.65	0.2252
C. July				
Site (PC vs. PB)	1	11	69.05	<.0001
Treatment (Control vs. Trim Early)	1	11	64.44	<.0001
Site x Treatment	1	11	11.63	0.0058
Slice				
Treatment PC	1	11	63.68	<.0001
Treatment PB	1	11	10.96	0.0069
D. September (PC only)				
Treatment (all four)	3	18	28.51	<.0001
Contrasts:				
Control vs. Trimmed (trim early, trim late, and trim twice)	1	18	59.39	<.0001
Timing (trim early vs. trim late)	1	18	18.14	0.0005
Frequency (trim early and trim late vs. trim twice)	1	18	8.97	0.0078
Frequency x Timing (trim early vs. trim twice and trim late vs. trim twice)	2	18	13.65	0.0002
E. October (PB only)				
Treatment (all four)	3	12	1.92	0.1803
Contrasts:				
Control vs. Trimmed (trim early, trim late, and trim twice)	1	12	4.02	0.0682
Timing (trim early vs. trim late)	1	12	0.89	0.3642
Frequency (trim early and trim late vs. trim twice)	1	12	0.63	0.4438
Frequency x Timing (trim early vs. trim twice and trim late vs. trim twice)	2	12	0.68	0.5238
F. November (PC only)				
Treatment (all four)	3	14	2.31	0.1211
Contrasts:				
Control vs. Trimmed (trim early, trim late, and trim twice)	1	14	0.57	0.4635
Timing (trim early vs. trim late)	1	14	5.47	0.0347
Frequency (trim early and trim late vs. trim twice)	1	14	0.80	0.3863
Frequency x Timing (trim early vs. trim twice and trim late vs. trim twice)	2	14	3.27	0.0682

Note: Data for this response variable were square root transformed. Refer to Table 1 for analysis details.

Table 5. Results from mixed model ANOVA of *Postelsia* percent sorus area.

	Num df	Den df	F	p-value
A. Spring (late April / mid May)				
Site (PC vs. PB)	1	11	10.62	0.0076
Treatment (Control vs. Trim Early)	3	22	0.41	0.7455
Site x Treatment	2	22	1.77	0.1933
B. June				
Site (PC vs. PB)	1	11	0.43	0.5275
Treatment (Control vs. Trim Early)	1	11	19.94	0.0010
Site x Treatment	1	11	0.07	0.7894
C. July				
Site (PC vs. PB)	1	11	5.19	0.0438
Treatment (Control vs. Trim Early)	1	11	26.02	0.0003
Site x Treatment	1	11	2.66	0.1315
D. September (PC only)				
Treatment (all four)	3	18	5.62	0.0067
Contrasts:				
Control vs. Trimmed (trim early, trim late, and trim twice)	1	18	7.36	0.0143
Timing (trim early vs. trim late)	1	18	1.72	0.2064
Frequency (trim early and trim late vs. trim twice)	1	18	7.99	0.0112
Frequency x Timing (trim early vs. trim twice and trim late vs. trim twice)	2	18	4.88	0.0202
E. October (PB only)				
Treatment (all four)	3	12	0.12	0.9437
Contrasts:				
Control vs. Trimmed (trim early, trim late, and trim twice)	1	12	0.16	0.6998
Timing (trim early vs. trim late)	1	12	0.03	0.8591
Frequency (trim early and trim late vs. trim twice)	1	12	0.17	0.6839
Frequency x Timing (trim early vs. trim twice and trim late vs. trim twice)	2	12	0.11	0.8969
F. November (PC only)				
Treatment (all four)	3	15	2.58	0.0924
Contrasts:				
Control vs. Trimmed (trim early, trim late, and trim twice)	1	15	0.02	0.8872
Timing (trim early vs. trim late)	1	15	7.65	0.0144
Frequency (trim early and trim late vs. trim twice)	1	15	0.01	0.9430
Frequency x Timing (trim early vs. trim twice and trim late vs. trim twice)	2	15	3.83	0.0453

Note: Data for this response variable were arcsine square root transformed. Refer to Table 1 for analysis details.

Table 6. Results from mixed model ANOVA of *Postelsia* spore production.

	Num df	Den df	F	p-value
A. Spring (late April / mid May)				
Site (PC vs. PB)	1	11	1.49	0.2477
Treatment (Control vs. Trim Early)	3	20	3.1	0.0501
Site x Treatment	2	20	0.88	0.4285
B. June				
Site (PC vs. PB)	1	11	1.53	0.2412
Treatment (Control vs. Trim Early)	1	11	67.43	<.0001
Site x Treatment	1	11	52	0.4839
C. July				
Site (PC vs. PB)	1	10	0.46	0.5117
Treatment (Control vs. Trim Early)	1	10	9.42	0.0119
Site x Treatment	1	10	1.61	0.2333
D. September (PC only)				
Treatment (all four)	3	18	7.45	0.0019
Contrasts:				
Control vs. Trimmed (trim early, trim late, and trim twice)	1	18	7.56	0.0132
Timing (trim early vs. trim late)	1	18	5.22	0.0346
Frequency (trim early and trim late vs. trim twice)	1	18	9.8	0.0058
Frequency x Timing (trim early vs. trim twice and trim late vs. trim twice)	2	18	7.37	0.0046
E. October (PB only)				
Treatment (all four)	3	10	1.62	0.2472
Contrasts:				
Control vs. Trimmed (trim early, trim late, and trim twice)	1	10	0	0.9541
Timing (trim early vs. trim late)	1	10	4.85	0.0523
Frequency (trim early and trim late vs. trim twice)	1	10	0	0.9911
Frequency x Timing (trim early vs. trim twice and trim late vs. trim twice)	2	10	2.42	0.1386
F. November (PC only)				
Treatment (all four)	3	11	3.22	0.0651
Contrasts:				
Control vs. Trimmed (trim early, trim late, and trim twice)	1	11	1.12	0.3129
Timing (trim early vs. trim late)	1	11	8.99	0.0121
Frequency (trim early and trim late vs. trim twice)	1	11	0.09	0.7638
Frequency x Timing (trim early vs. trim twice and trim late vs. trim twice)	2	11	4.5	0.0372

Note: Data for this response variable were $Log_{10}+1$ transformed. Refer to Table 1 for analysis details.

Table 7. Results from mixed model ANOVA of *Postelsia* spore viability.

	Num df	Den df	F	p-value
A. Spring (late April / mid May)				
Site (PC vs. PB)	1	3	3.12	0.1755
Treatment (Control vs. Trim Early)	1	3	0.56	0.5093
Site x Treatment	1	3	1.4	0.3217
B. June				
Site (PC vs. PB)	1	8	0.69	0.4292
Treatment (Control vs. Trim Early)	1	8	2.61	0.1445
Site x Treatment	1	8	0.43	0.5320
C. July				
Site (PC vs. PB)	1	6	5.38	0.0595
Treatment (Control vs. Trim Early)	1	6	0.02	0.8943
Site x Treatment	1	6	2.24	0.1852
D. September (PC only)				
Treatment (all four)	3	18	6.58	0.0034
Contrasts:				
Control vs. Trimmed (trim early, trim late, and trim twice)	1	18	4.85	0.0409
Timing (trim early vs. trim late)	1	18	14.06	0.0015
Frequency (trim early and trim late vs. trim twice)	1	18	0.76	0.3936
Frequency x Timing (trim early vs. trim twice and trim late vs. trim twice)	2	18	7.41	0.0045
E. October (PB only)				
Treatment (all four)	3	11	9.39	0.0023
Contrasts:				
Control vs. Trimmed (trim early, trim late, and trim twice)	1	11	4.86	0.0497
Timing (trim early vs. trim late)	1	11	13.36	0.0038
Frequency (trim early and trim late vs. trim twice)	1	11	9.07	0.0118
Frequency x Timing (trim early vs. trim twice and trim late vs. trim twice)	2	11	11.89	0.0018
F. November (PC only)				
Treatment (all four)	3	15	2.34	0.1151
Contrasts:				
Control vs. Trimmed (trim early, trim late, and trim twice)	1	15	2.67	0.1229
Timing (trim early vs. trim late)	1	15	0.25	0.6238
Frequency (trim early and trim late vs. trim twice)	1	15	4.15	0.0597
Frequency x Timing (trim early vs. trim twice and trim late vs. trim twice)	2	15	2.18	0.1473

Note: Data for this response variable were arcsine square root transformed. Refer to Table 1 for analysis details.

Table 8. Results from mixed model ANOVA of *Postelsia* number of viable spores (0.125 m^2).

	Num df	Den df	F	p-value
A. Spring (late April / mid May)				
Site (PC vs. PB)	1	1	2.09	0.3851
Treatment (Control vs. Trim Early)	1	1	0.69	0.5587
Site x Treatment	1	1	0.69	0.5587
B. June				
Site (PC vs. PB)	1	7	1.55	0.2530
Treatment (Control vs. Trim Early)	1	7	6.57	0.0374
Site x Treatment	1	7	0.24	0.6423
C. July				
Site (PC vs. PB)	1	6	0.23	0.6463
Treatment (Control vs. Trim Early)	1	6	0.79	0.4079
Site x Treatment	1	6	0.65	0.4501
D. September (PC only)				
Treatment (all four)	3	18	18.30	<.0001
Contrasts:				
Control vs. Trimmed (trim early, trim late, and trim twice)	1	18	29.70	<.0001
Timing (trim early vs. trim late)	1	18	21.30	0.0002
Frequency (trim early and trim late vs. trim twice)	1	18	5.42	0.0318
Frequency x Timing (trim early vs. trim twice and trim late vs. trim twice)	2	18	13.40	0.0003
E. October (PB only)				
Treatment (all four)	3	10	1.44	0.2878
Contrasts:				
Control vs. Trimmed (trim early, trim late, and trim twice)	1	10	3.96	0.0747
Timing (trim early vs. trim late)	1	10	0.19	0.6728
Frequency (trim early and trim late vs. trim twice)	1	10	0.09	0.7700
Frequency x Timing (trim early vs. trim twice and trim late vs. trim twice)	2	10	0.13	0.8772
F. November (PC only)				
Treatment (all four)	3	11	0.89	0.4788
Contrasts:				
Control vs. Trimmed (trim early, trim late, and trim twice)	1	11	1.02	0.3336
Timing (trim early vs. trim late)	1	11	1.77	0.2098
Frequency (trim early and trim late vs. trim twice)	1	11	0.00	0.9505
Frequency x Timing (trim early vs. trim twice and trim late vs. trim twice)	2	11	0.89	0.4390

Note: Data for this response variable were square root transformed. Refer to Table 1 for analysis details.

Figures
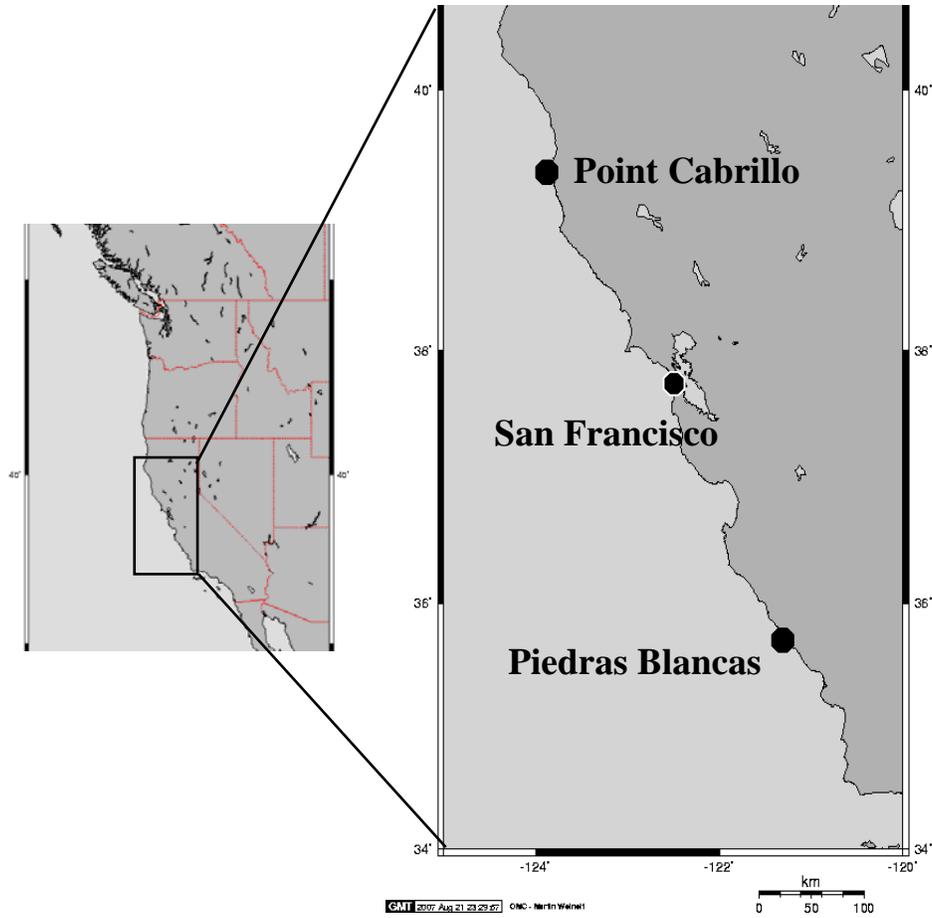
Figure 1. Location of study sites in California, USA.

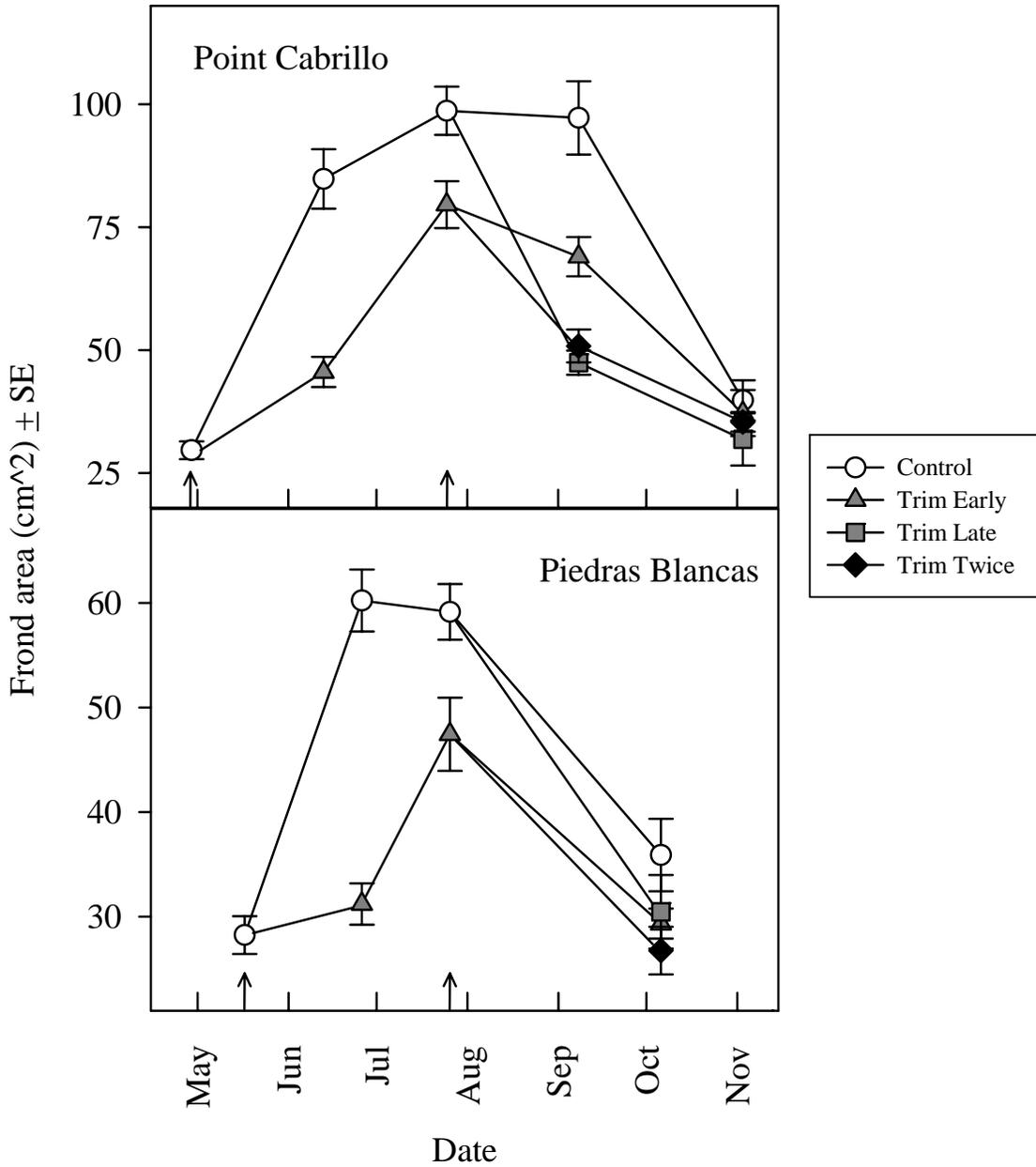Figure 2. *Postelsia* density (number of plants per 0.125 m^2) by treatment over time in 2006. Means and standard errors are back transformed to linear scale from the square root scale used for statistical analysis. Fronds were trimmed leaving the meristem intact, allowing for regrowth. Treatments tested timing and frequency of trimming: one trimming early in the season (trim early), one trimming late in the season (trim late), or trimming early and repeated on late trimming date (trim twice). Arrows indicate time of trimmings.
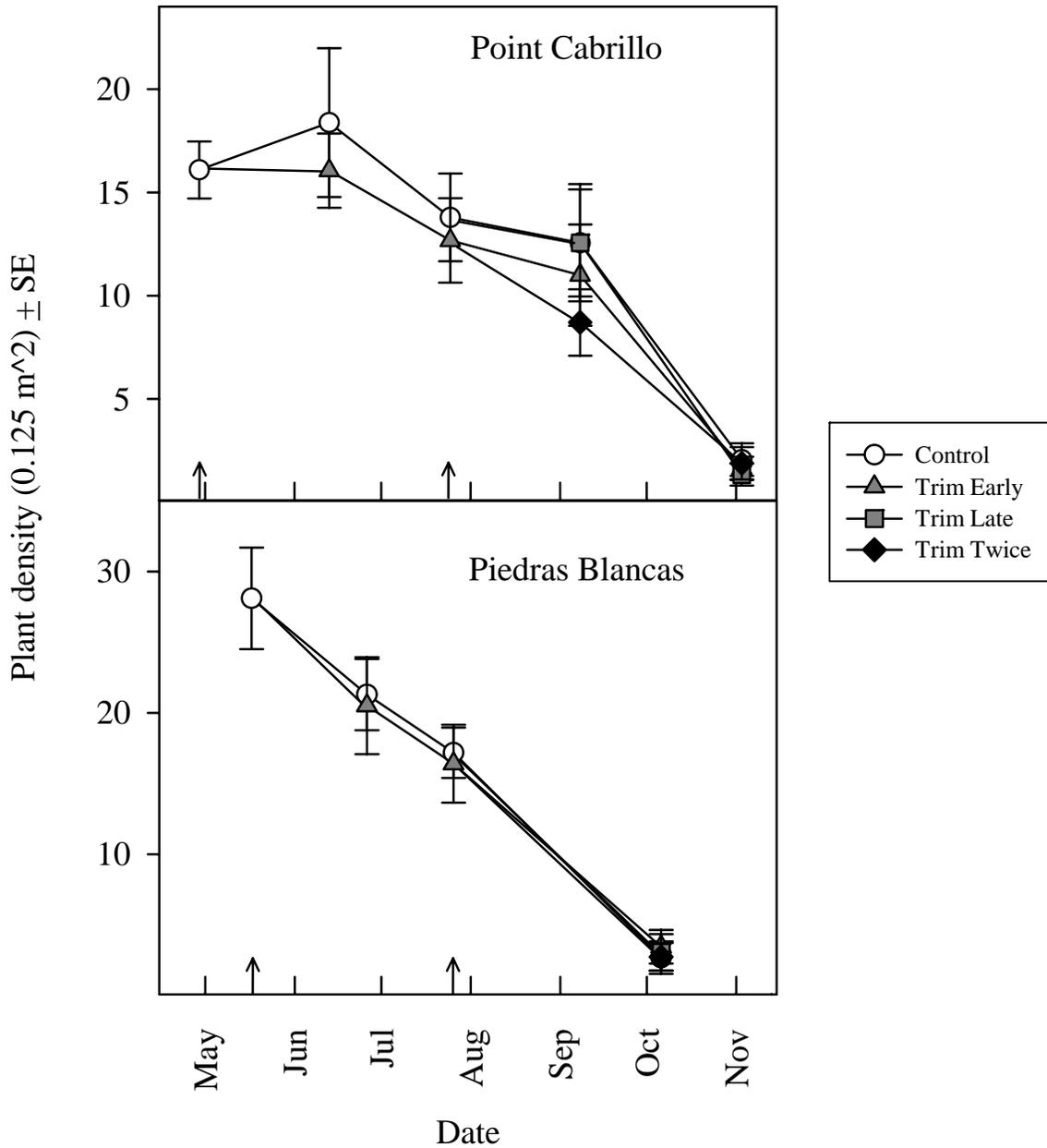
Figure 3. *Postelsia* frond length by treatment over time in 2006. Means and standard errors are back transformed to linear scale from the Log_{10} scale used for statistical analysis. Refer to Fig. 2 caption for trimming treatment information.
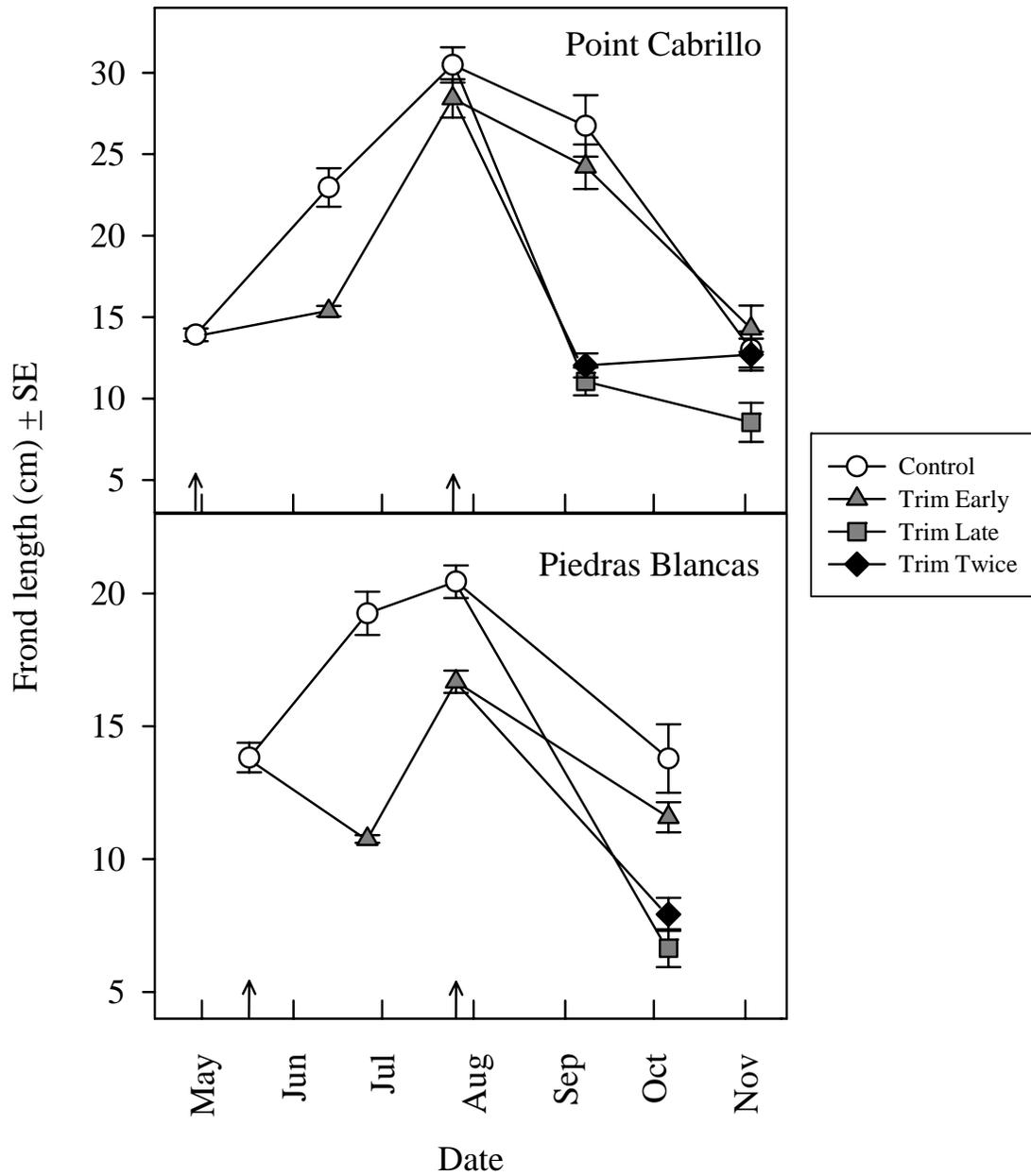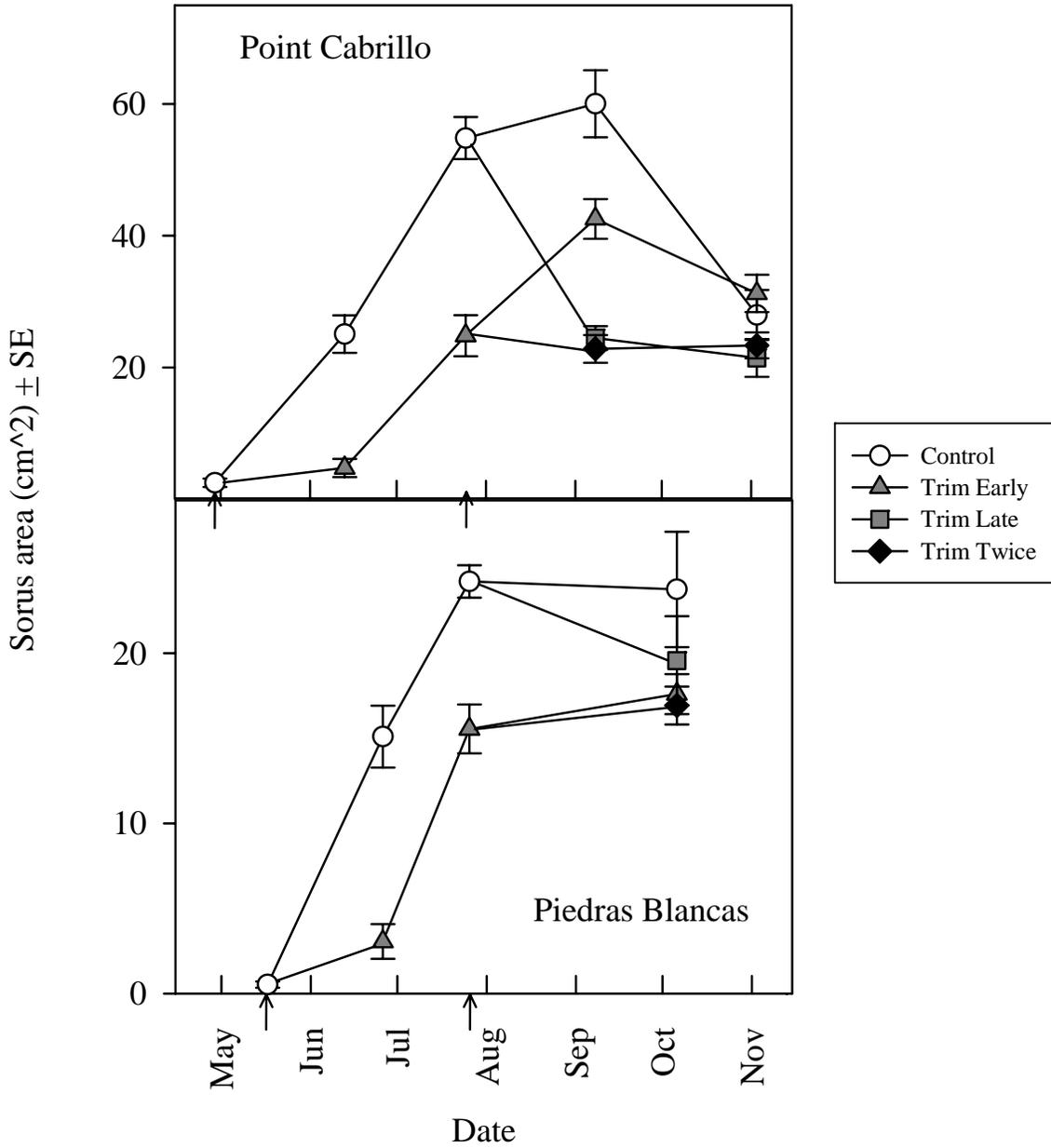
Figure 4. *Postelsia* frond area by treatment over time in 2006. Means and standard errors are back transformed to linear scale from the Log_{10} scale used for statistical analysis. Refer to Fig. 2 caption for trimming treatment information.

Figure 5. *Postelsia* sorus area by treatment over time in 2006. Means and standard errors are back transformed to linear scale from the square root scale used for statistical analysis. Refer to Fig. 2 caption for trimming treatment information.

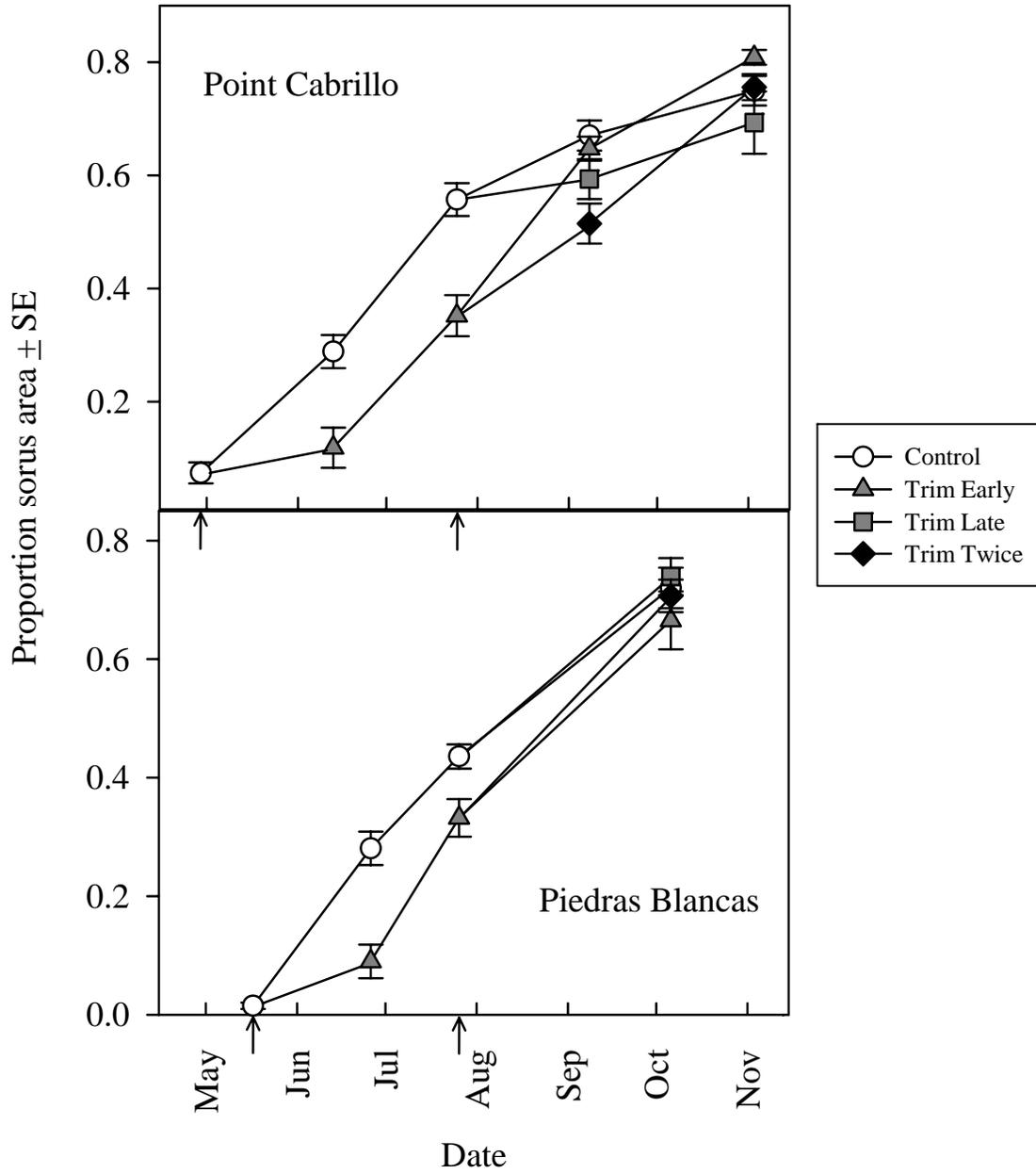Figure 6. *Postelsia* proportion sorus area by treatment over time in 2006. Means and standard errors are back transformed to linear scale from the arcsine square root scale used for statistical analysis. Refer to Fig. 2 caption for trimming treatment information.

Figure 7. *Postelsia* spore production by treatment over time in 2006. Means and standard errors are presented on the Log scale. Refer to Fig. 2 caption for trimming treatment information.
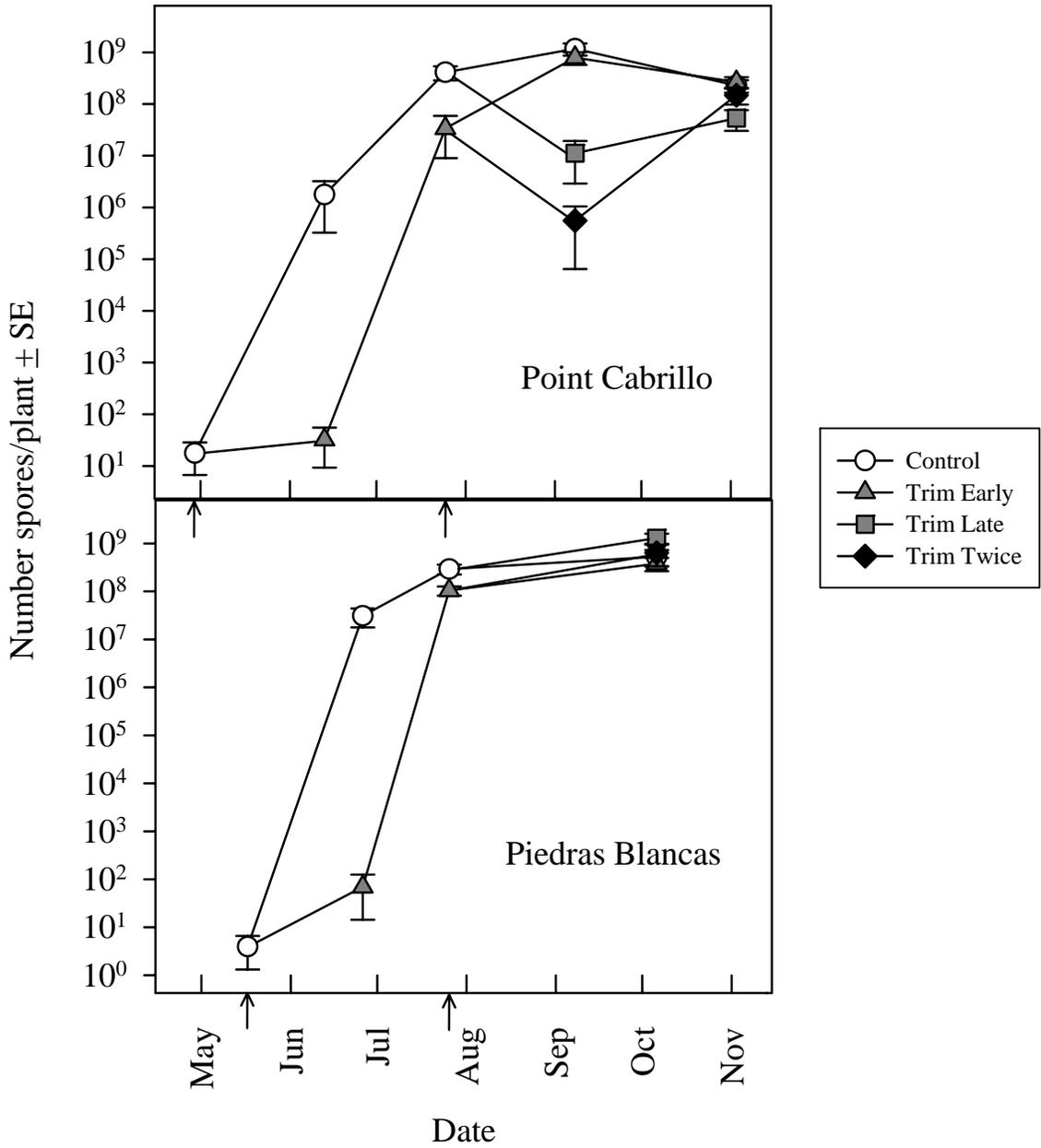
Figure 8. Spore production as predicted by sorus area. Circular symbols code immature individuals that are not yet shedding spores, and are not included in the regressions. Black symbols and regression are from PC ($p < 0.0001$; $r^2 = 0.70$; Log$_{10}$ (no. spores/plant + 1) = 4.12 + 2.69 Log$_{10}$ (sorus area)) and gray symbols and regression are from PB ($p < 0.0001$; $r^2 = 0.64$; Log$_{10}$ (no. spores/plant + 1) = 4.06 + 3.34 Log$_{10}$ (sorus area)). The inset figure expresses the same spore production data on a different scale and clearly indicates a sorus area threshold (8.31 cm^2) beyond which spore release increases dramatically (note that the critical threshold area is somewhat larger at PC).
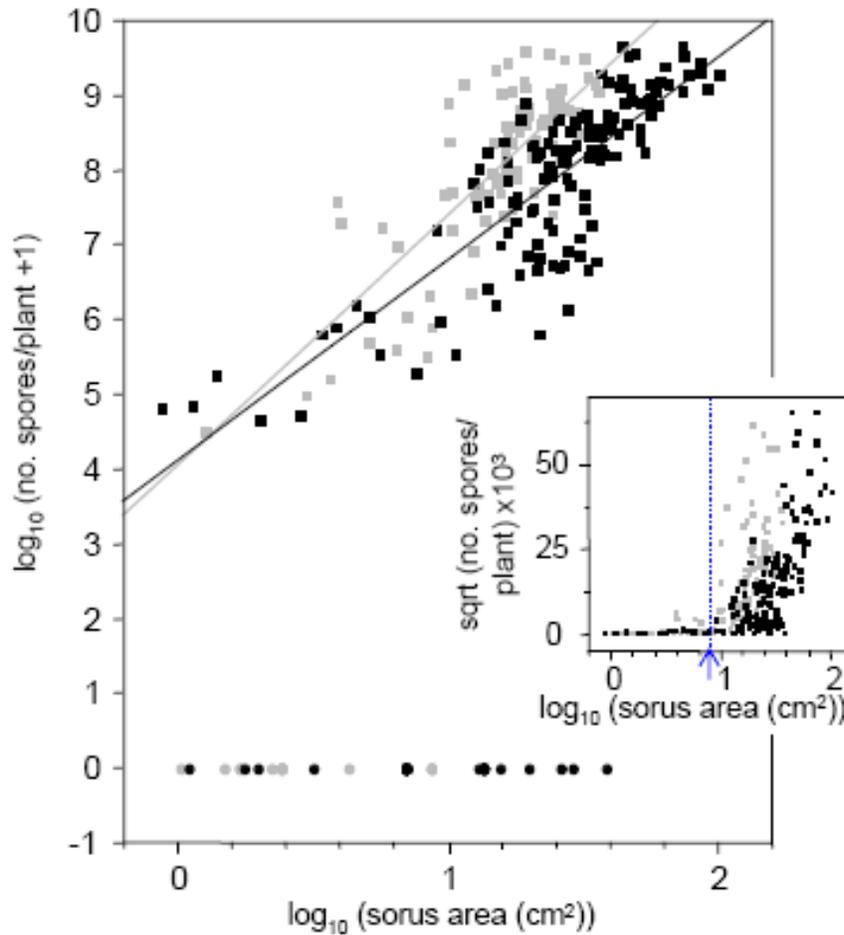
Figure 9. *Postelsia* germination success by treatment over time in 2006. Means and standard errors are back transformed to linear scale from the arcsine square root scale used for statistical analysis. Refer to Fig. 2 caption for trimming treatment information.
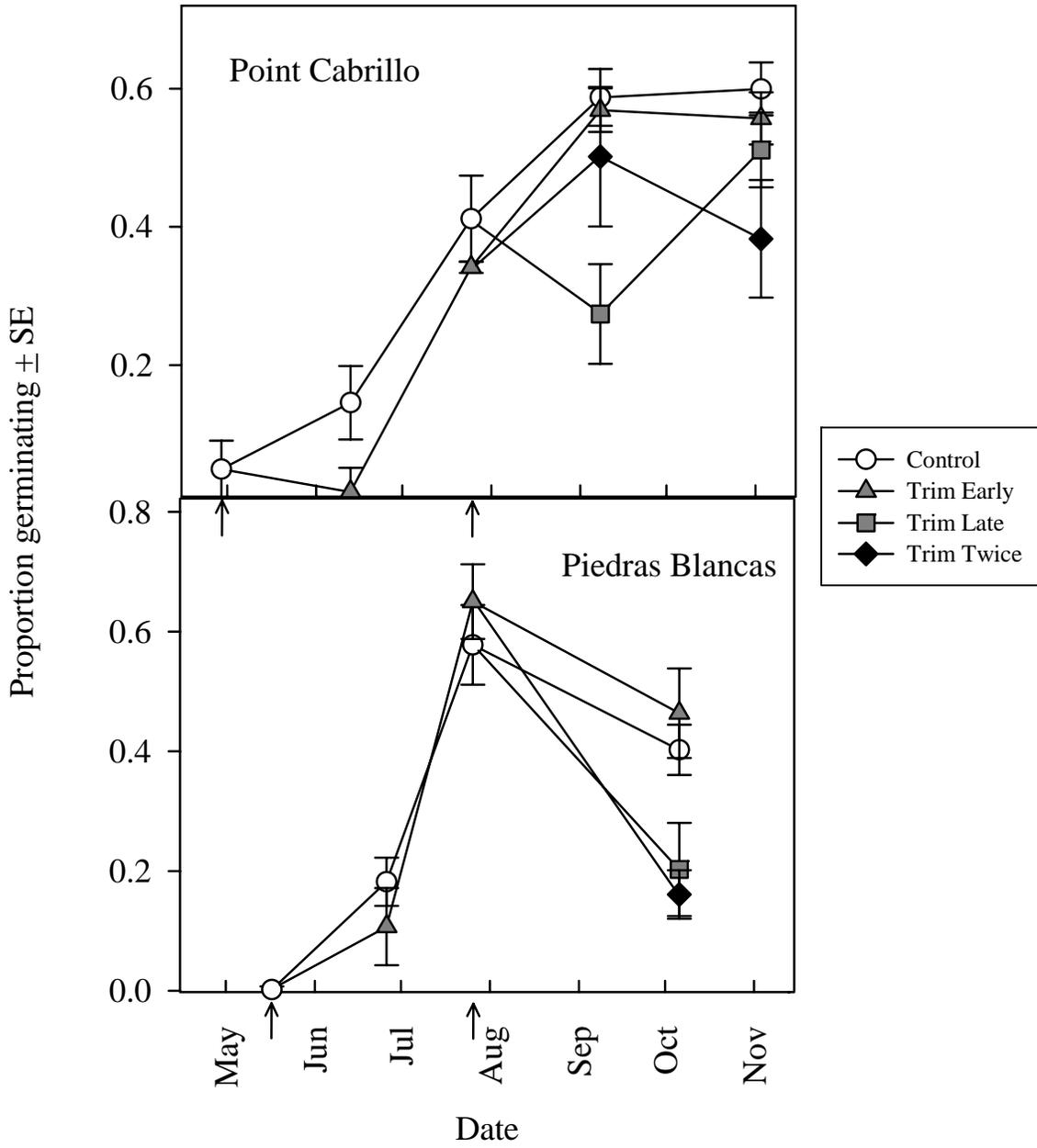
Figure 10. *Postelsia* number of viable spores released per 0.125 m^2 by treatment over time in 2006. Means and standard errors are back transformed to linear scale from the square root scale used for statistical analysis. Refer to Fig. 2 caption for trimming treatment information.