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**Effects of prescribed fires on young valley oak trees
at a research restoration site in the Central Valley of California**

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Running head: Effects of prescribed fires on young restored oaks

1 **ABSTRACT**

2 Woodland restoration sites planted with *Quercus lobata* (valley oak) often have serious invasions
3 of nonnative annual grasses and thistles. Although prescribed fire can effectively control these
4 exotics, restoration managers may be reluctant to use fire if it causes substantial mortality of
5 recently-planted saplings. We studied the effects of prescribed fires on the survival and
6 subsequent growth of five- and six-year-old valley oak saplings at a research field near Davis,
7 California. One set of blocks was burned in summer 2003 at a time that would control yellow
8 star thistle, a second set of blocks was burned in spring 2004 at a time that would control annual
9 grasses, and a third set was left unburned. Very few oaks died as a result of either fire (3-4%).
10 Although a large proportion were top-killed (66-72%), virtually all these coppiced, and most
11 saplings over 300 cm tall escaped top-kill. Tree height, fire temperature, and understory biomass
12 were all predictive of the severity of sapling response to fire. Although mean sapling height was
13 initially reduced by the fires, the growth rates of burned saplings significantly exceeded the
14 growth rates of unburned control trees for two years following the fires. By two to three years
15 after the fires, the mean height of spring- and summer-burned saplings was similar to that of the
16 unburned control saplings. The presence of valley oak saplings does not appear to preclude the
17 use of a single prescribed burn to control understory invasives, particularly if saplings are over
18 300 cm tall.

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20 *Keywords:* prescribed burn, prescribed fire, *Quercus lobata*, valley oak, top-kill, basal sprout

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1 INTRODUCTION

2 Oak woodlands in California have been greatly reduced in the last one hundred years, and
3 the vast riparian woodlands dominated by *Quercus lobata* (valley oak) have been almost
4 completely eliminated by conversion to cropland and development (Vaghti and Greco 2007,
5 Katibah 1984). In addition, surviving oak populations of many species exhibit severe long-term
6 recruitment failures that have created stands virtually devoid of saplings and young trees (Griffin
7 1976, Bolsinger 1988). In recent years, there has been considerable effort at restoring oak
8 woodlands, and valley oaks are one of the most frequently planted trees at riparian restoration
9 sites in the Central Valley (Young and Evans 2005).

10 Although natural oak stands often exhibit recruitment failure, the establishment of young
11 valley oak saplings through active restoration has met with widespread success, but the
12 establishment of native understories in these ecosystems has been severely hampered by invasive
13 annual plants such as *Aegilops triuncialis* (goatgrass), *Taeniatherum caput-medusae*
14 (medusahead), and *Centaurea solstitialis* (yellow star-thistle) (Stromberg et al. 2007). One of
15 the more successful tools for dealing with these invasives is fire (DiTomaso et al. 2006), which is
16 increasingly being used in strategies to restore Central Valley grasslands (Stromberg et al. 2007,
17 Lulow et al. 2007). However, in sites where oak saplings have been planted, there is concern
18 about the effects of fire on these young trees (Swiecki & Bernhardt 1998; Mitch Sears, Chris
19 Alford, Jeremiah Mann, pers. comms.).

20 There are reasons to believe that these communities, and oak trees in particular, have
21 evolved in a naturally fire-prone ecosystem and survived anthropogenic fires for many centuries.
22 Plant communities in California's Mediterranean climate have probably always endured fires
23 (Greenlee and Langenheim 1990), and many of its plant species, including most oaks, exhibit
24 adaptations to fire, such as basal sprouting and thick bark (Pavlik et al. 1991), similar to other

1 woodland and savanna species worldwide (Gignoux et al. 1997, Bond and Midgley 2000,
2 Hoffmann and Solbrig 2003). Native Americans are thought to have set frequent, low intensity
3 fires in Central Valley grasslands and oak woodlands up until the 1800's (Greenlee and
4 Langenheim 1990, Wills 2006). With the 1948 gold rush and the concomitant increased in
5 ranching, fire frequency initially increased, but fire suppression eventually became the norm
6 (Biswell 1989, McClaran and Bartolome 1989, Wills 2006), and now fires in California's oak
7 woodlands are rare (Greenlee and Langenheim 1990). The effects of fire on oak recruitment and
8 mortality are still not fully understood (Barbour and Minnich 2000; Holmes et al. *in press*) and
9 there is disagreement about the appropriate ways to reintroduce fire into oak woodlands (Biswell
10 1989, Bartolome et al. 2002). Similar restoration of woody species is common in fire-prone
11 communities with Mediterranean climates worldwide (Cione et al. 2002, Pausas et al. 2004,
12 Benayes et al. 2004, Midoko-Iponga et al. 2005, Sanchez-Gomez et al. 2006, Alvarado-Sosa et
13 al. 2007.)

14 There are several potential benefits to reintroducing fire into California's oak
15 communities. Many of the exotic species invading California's oak woodlands and grasslands
16 are not adapted to fire (especially spring and early summer fire), and controlled burns have
17 proven effective in controlling common understory exotics such as *Cytisus scoparius* (Scotch
18 broom), yellow star thistle and various annual grasses (Bossard et al. 2000, DiTomaso et al.
19 2006). Wildfire can also increase the presence of fire-adapted native species in the understory of
20 oak woodlands (Dagit 2002) and reduce levels of the parasitic oak mistletoe *Phoradendron*
21 *villosum* (Haggerty (1994).

22 Fire may directly promote the establishment of oak seedlings, perhaps by reducing
23 competitive pressure from understory vegetation, releasing soil nutrients, reducing litter-born
24 pathogens, or improving contact with mineral soils. There is evidence that fire increases the

1 recruitment of *Q. kelloggii* (black oak) (Kauffman and Martin 1987) and *Q. garryana* (Oregon
2 white oak) (Regan and Agee 2004), although the same has not been found for *Q. douglasii* (blue
3 oak) (Allan-Diaz and Bartolome 1992) or valley oak (Swiecki and Bernhardt 1998).

4 Unfortunately reintroduction of fire is not without risk. Although mature individuals of
5 many oak species usually survive fires, seedling and saplings are at greater risk. A survey of
6 studies investigating the effects of fire on seven different species of California oak species found
7 that mortality rates generally ranged between 1 to 11 percent for mature oaks, 2 to 10 percent for
8 sapling oaks, and 17 to 52 percent for seedling oaks (Holmes et al. *in press*). Although fire does
9 not usually cause complete death of sapling oaks, it does result in top-kill 75-90% of the time
10 (Holmes et al. *in press*). Top-kill occurs when above-ground portions of saplings die, but
11 subsequently recover via sprouting of new basal coppice shoots (Fry 2008). Even if these basal
12 sprouting individuals survive fire, they are at risk of damage from deer browsing or subsequent
13 fires until their coppice shoots grow up through susceptible height classes (Bartolome et al. 2002,
14 Swiecki and Bernhardt 2002).

15 Several studies have investigated the effects of fire on non-sapling-sized valley oaks
16 (Griffen 1980, Schwan et al. 1997, Fry 2008). However, no studies have comprehensively
17 examined the effects of fire on sapling-aged valley oak individuals (Holmes et al. *in press*), nor
18 of planted young oaks in a restoration setting. Newly-planted valley oak stands often have
19 understories dominated by invasive annuals that limit the restoration of functioning oak
20 woodland communities. Although prescribed burning can effectively control exotic grasses and
21 thistles, there is reluctance to burn restoration-stage oak plantings because of uncertainty over the
22 effects of such burns on the young planted oaks (Swiecki & Bernhardt 1998; Chris Alford, Mitch
23 Sears, pers. comm.).

1 The purpose of this study was to: 1) investigate the response of sapling valley oaks to late
2 spring and early summer prescribed fires; 2) identify predictors of sapling valley oak fire
3 response and develop critical thresholds for mortality and top kill; and 3) determine post-fire
4 growth rate and height recovery of valley oak saplings.

6 **METHODS**

7 **Study site** Our study site was a two hectare research field near Davis, California
8 (38°31'26"N, 121°45'31"W). It experiences a Mediterranean climate, with rain restricted to
9 winter months. Mean annual rainfall is 18" (462 mm). Total winter rainfalls in 2003/4 and
10 2004/5 were 14.2" (360 mm) and 21.8" (554 mm), respectively. The original vegetation was
11 likely valley oak woodland.

12 The site was planted with several hundred valley oak acorns and seedlings in the winter
13 of 1999 as part of a separate restoration experiment (Hobbs and Young 2001, Young and Evans
14 2001, 2005). The original experiment was divided into 54 plots of nine oaks each, which
15 received different combinations of planting stock (seed vs. container stock), and irrigation (none,
16 one year, or two years). The experiment concluded in 2000 and 278 trees remained at the site by
17 spring 2003. There had been no weed control or supplemental irrigation since 2000.

18 There was no overstory canopy layer at the site other than the planted oaks and the
19 understory layer was dominated by nonnative annual grasses (including *Bromus diandrus*, *Avena*
20 *barbata*, *Lolium multiflorum* and *Hordeum murinum*) and *Centaurea solstitialis* (yellow star
21 thistle).

22 **Burn blocks and tree heights** There were still some residual differences in tree size due
23 to the previous restoration experiment, which we mitigated in two ways. First, we combined
24 pairs of adjacent plots (with different experimental histories) into 27 blocks of 72 m² each, with

1 an average of ten trees per block. Second, the burn treatments assigned to these blocks were
2 stratified across previous experimental history and regularly interspersed. Nine blocks were
3 assigned a summer burn treatment, nine were assigned a spring burn treatment, and nine were
4 left unburned as a control. Of these 27 blocks, one (a control) had only three small trees (mean
5 2003 height, 49cm), and was excluded from analysis. The net result was three sets of 8-9 fire
6 treatment blocks that were similar in mean tree size and variance in tree size (see Figure 1).

7 The two burn treatments were carried out at two different times of year, but were also
8 each carried out once and in different years, so are not a direct test for the effects for burn timing
9 (or year effects, or tree age). However, their consistent effects do add a greater confidence in the
10 generality of our conclusions. We called them Summer03 and Spring04 burns here to emphasize
11 these multiple factors.

12 **Summer 2003 burn** In April 2003, the height was measured for all trees in all three
13 treatments. For those trees included in the Summer03 burn treatment, the grass biomass under
14 each tree was assigned a density level of one (low) through five (high). Ceramic tiles painted
15 with five different temperature-sensitive welding paints (at regular intervals between 79°C and
16 399°C) were hung at a height of 30 centimeters on each of the 88 Summer03-burn trees. Three
17 weeks after the burn, the height of the top of the scorch level was measured for each tree. Three
18 months after the burn, the survivorship of the main leader was assessed and the number of
19 coppice sprouts and height of the tallest coppice were measured for each tree.

20 The Summer03 burn was conducted on July 16, 2003 from 12:00 pm until 4:00 p.m.
21 During the burn, dry bulb temperatures averaged 34°C and average relative humidity was 37%.
22 As recorded by the ceramic tiles, fire temperatures reached a high of 204°C with a mean of 95°C.
23 Most of the litter and understory herb layer was consumed, although some patchiness was
24 evident with small areas of litter only lightly charred. Fire carried into the crowns of many of the

1 saplings and 26% percent of all individuals experienced 100% crown scorch, although leaves and
2 small twigs were only rarely completely consumed by the fire.

3 **Spring 2004 burn** In May 2004, height measurements were taken again for all trees in
4 all three treatments. Pre- and post-burn measurements similar to those described above for
5 Summer03 burn trees were taken for all Spring04 burn trees. Aluminum tags painted with five
6 different temperature-sensitive paints (at regular intervals between from 79°C and 232°C) were
7 again used to measure fire temperature at each of the 94 Spring04-burn trees. In addition to the
8 aluminum tags, ceramic tags with the same paints were hung on 18 trees, to compare these two
9 monitoring methods.

10 The Spring04 burn was conducted on May 28, 2004 from 11:00 am until 3:00 pm.
11 During the burn, dry bulb temperatures averaged 23°C and average relative humidity was 58%.
12 As recorded by the aluminum tags, fire temperatures reached a high of at least 232°C with a
13 mean of 197°C. For the 18 trees with both aluminum tags and ceramic tiles, mean aluminum tag
14 temperature was 194°C and mean ceramic tile temperature was 141°C. As with the Summer03
15 burn, the litter and understory herb layer was mostly consumed, although patchiness was evident.
16 High spring precipitation had created lush and uniform understory growth in 2004. Fuel ladders
17 carried fire into the crowns of most of the saplings with 66 percent experiencing 100% crown
18 scorch. As with the Summer03 burn, leaves and small twigs were usually not completely
19 consumed by the fire.

20 **Follow up measurements** In November 2005 and again in September 2006, the height
21 was measured for all saplings in all three treatments, and main leader mortality and number of
22 coppice sprouts were noted.

23 **Statistical analysis** Proportion of trees with different fire responses and mean heights
24 for each year were calculated for each treatment block. Differences in sapling response to fire

1 among the three treatments were compared with ANOVA, treating the nine fire blocks per
2 treatment as replicates (eight replicates for controls).

3 Pre-burn tree height turned out to be a very strong correlate of tree fate (see Figures 2 and
4 3), and averaging responses across trees within blocks would negate the most important covariate
5 of fate for subsequent predictor analyses. We therefore used individual tree measurements in the
6 multiple logistic regression analysis described below. Statistically, this means we treated all of
7 the blocks within a given treatment as a single burn. Such pseudo-replication is not uncommon
8 when doing difficult fire experiments (Van Mantgem et al. 2001), and we were at least partly
9 protected from bias by the fact that the blocks we analyzed together had been previously
10 stratified and interspersed in a way that minimized potentially misleading block effects (see
11 above).

12 We used multiple logistic regression to determine significant predictors of saplings'
13 responses to fire. We used tree size, understory grass biomass class, and fire temperatures as
14 predictors. In order to attain the minimum count and expected cell count frequencies necessary
15 for statistical analyses, the two more-severe response categories (death and top-kill) were
16 combined. McFadden's ρ^2 values were used to determine the degree of correlation between
17 predictive factors and tree response. Although McFadden's ρ^2 values are similar to the R^2 values
18 of linear regression, they tend to be much lower and are considered highly satisfactory in the
19 range of 0.2-0.4 (Tabachnick and Fidell 2001). Likelihood ratio tests were used to determine
20 which predictive factors were making significant contributions to the multiple logistic regression
21 model.

22 Relative growth rates (RGR) of tree heights were used to compare the growth of burned
23 trees versus control trees. The RGR during the first time interval following fire was calculated
24 by (final height – postburn height) / preburn height. The RGR of subsequent time intervals was

1 calculated by (final height - initial height) / initial height. Mean RGR values for each block were
2 calculated for each time interval. Growth rate comparisons (both RGR and absolute height)
3 among fire treatments were made using ANOVA, treating the eight or nine fire blocks per
4 treatment as replicates.

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7 **RESULTS**

8 **Sapling response to fire** The burns resulted in three levels of sapling response, with the
9 most severe being entire tree death, followed by top-killed trees (dead main leader with sprouts
10 from the tree base), and trees that still had live main leaders (**Table 1**). Very few of the valley
11 oak saplings died as a result of either fire (3-4%), although the majority were top-killed (66-
12 72%). During the same time period, none of the control trees died or were top-killed. Basal
13 sprouting was greatly increased by the burns, averaging 4.6 sprout per tree, compared with less
14 than one per tree in the control plots ($p < 0.001$). The latter was likely related to stem damage by
15 small mammals.

16 **Predictors of sapling response to fire and critical thresholds** Multiple logistic
17 regression indicated that a combination of preburn height, understory biomass and fire
18 temperature significantly predicted tree response to fire (**Table 2**). Each of these three factors
19 also independently affected the severity of burn effects. For both Summer03 and Spring04 fires,
20 smaller trees were more likely to exhibit a more severe burn response (either death or top-kill)
21 than larger trees (**Table 2**). Fire temperature was also a good predictor of tree response to fire,
22 with higher temperatures predictive of a more severe response (**Table 2**). Understory biomass
23 class was only a weakly significant predictor, and only for the Summer03 burn, with trees

1 growing in higher density understory biomass classes somewhat more likely to experience a
2 severe response (**Table 2**).

3 The Summer03-burned trees did not have any height classes where all individuals
4 avoided being top-killed by the fire (**Figure 2**), while all Spring04-burned trees greater than 300
5 cm avoided being top-killed by the prescribed burn (**Figure 3**). Of the seven trees that died in
6 the fires, four were less than one meter tall and all were less than 1.5 meters tall.

7 **Relative growth rates (RGR) and recovery of height** Both Summer03- and Spring04-
8 burned trees grew faster than the control trees for the first two years after their respective fires.
9 The Summer03-burned trees' average RGR was significantly higher than controls during the first
10 year (0.46 ± 0.05 vs. 0.27 ± 0.05 ; $F=7.91$, $p=0.013$) and second year (1.57 ± 0.11 vs. 0.74 ± 0.12 ;
11 $F=26.3$, $p<0.001$), but did not differ significantly during the third year (0.44 ± 0.06 vs. $0.39 \pm$
12 0.03 ; $F=0.63$, $p=0.44$). For Spring04 burned trees, average RGR was (non-significantly) higher
13 during the first year (1.00 ± 0.13 vs. 0.74 ± 0.12 ; $F=2.14$, $p=0.16$) and significantly higher in the
14 second year (0.54 ± 0.03 vs. 0.38 ± 0.03 ; $F=16.60$, $p=0.001$). By September 2006, both
15 Summer03- and Spring04-burned trees had returned to heights similar to those of unburned
16 control trees (**Figure 1**, $F=0.72$, $p=0.50$).

17

18 **DISCUSSION**

19 The valley oak saplings in this experiment experienced very low mortality rates but
20 relatively high top-kill rates when exposed to a single low-to-moderate intensity prescribed fire,
21 a pattern typical of saplings of other California oak species (Holmes et al. *in press*). Saplings
22 were more likely to survive prescribed fire when they were larger, were exposed to lower burn
23 temperatures, or were surrounded by less-dense understory biomass.

1 Larger oak trees in general are more likely to survive fires (Paysen and Narog 1993,
2 Horney et al. 2002, Swiecki and Bernhardt 2002, Regan and Agee 2004), as were the larger
3 saplings in our study. Presumably, larger trees have thicker bark, which insulates and reduces
4 the amount of time living cells in the cambium layer are exposed to potentially lethal
5 temperatures (Hare 1965, Plumb 1980). In addition, larger individuals may have less flammable
6 twig and leaf material near the ground, because self-pruning produces bare lower trunks.
7 Establishing critical size thresholds at which sapling oaks are known to escape death and top-kill
8 is important for land managers who want to use prescribed fire as a restoration tool to control
9 exotics without detrimentally impacting young trees (Swiecki and Bernhardt 2002). Our study
10 indicates that valley oak saplings over 300 cm tall are unlikely to be top-killed in a low-to-
11 moderate prescribed fire. Since very few of even the smaller saplings experienced complete
12 mortality in either the Summer03 or the Spring04 burn, it does not appear that valley oak
13 saplings need to attain a minimum threshold size to avoid death by prescribed fire.

14 Both ambient temperatures and fuel moisture levels, two factors relating directly to
15 season of burn can influence the degree of fire-induced damage to oak trees. Summer burns may
16 be more severe because the higher ambient temperatures present during summer fires can result
17 in internal tree temperatures increasing to lethal levels much more rapidly compared with the
18 lower ambient temperatures present during early season fires (Hare 1965). Additionally the low
19 fuel moisture levels present during summer fires can create more intense fire conditions (Whelan
20 1995). Properties of trees' natural defenses may also interact with season to influence
21 susceptibility. Trees may retain higher bark moisture during earlier seasons (DeBano et al.
22 1998). This may provide some resistance against fire (Plumb 1980, but see DeBano et al. 1998).
23 However, in our study we did not find significant differences in overall survival or top-kill in the
24 summer and spring burns.

1 Although we found understory biomass class to be only a weakly significant predictor of
2 fire severity response, others have found that fuel loads do contribute to the level of fire damage
3 sustained by oaks (Kauffman and Martin 1987, Tietje et al. 2001). Higher density understory
4 biomass not only provides more fuel, thereby increasing fire temperatures, but also serves as a
5 fuel ladder, carrying flames into tree crowns and increasing the potential severity of a fire's
6 effects. One potential explanation for why understory biomass class was a better predictor for
7 our Summer03 burn than our Spring04 burn is that there was very little variation in understory
8 biomass in the Spring04 burn. High precipitation in spring 2004 created much more uniform and
9 high-density biomass levels throughout the Spring04 burn blocks than was found in the
10 Summer03 burn blocks.

11 Our study did not test the effects of multiple burns on valley oak sapling mortality and
12 top-kill. Other oak species subjected to multiple prescribed fires within a relatively short period
13 of time may experience higher levels of mortality (Peterson and Reich 2001, Regan and Agee
14 2004, Dey and Hartman 2005). Conversely, adult (but not sapling) trees in frequently burned
15 areas may instead show lower mortality if frequent burning leads to lower fire intensity
16 (Hutchinson et al. 2005). Although multiple burns are particularly effective in controlling annual
17 grasses or star thistle, even a single burn followed up by spot herbicide treatments can
18 substantially reduce cover by invasives, because many have very short-lived seed banks
19 (DiTomaso et al. 2006), and future re-invasion can be greatly reduced by aggressive planting of
20 native herbaceous species (Stromberg et al. 2007; John Anderson, pers. comm.). Further studies
21 are needed to test whether multiple burns will have negative direct effects on valley oak saplings
22 in restoration settings in the Central Valley.

23 The valley oak saplings in our study experienced rapid postburn growth for two years
24 following the fire, essentially recovering their height losses from the burns. Several other studies

1 (McClaran and Bartolome 1989, Bartolome et al. 2002, Swiecki and Bernhardt 2002, Brose and
2 Van Lear 1998) have also found that oaks experience accelerated post-fire growth. Accelerated
3 growth in other studies did not result in burned oaks returning within a few years to the full
4 height they would have been had they not been burned, perhaps because of shading from
5 overstory trees (Dey and Hartman 2005). Most restoration sites in the Central Valley are not light
6 limited, including ours, which may partially explain the rapid height recovery exhibited by
7 saplings in our study. It should also be noted that browsing deer or livestock populations (not
8 present at our site) can significantly slow height recovery (McClaran and Bartolome 1989,
9 Bartolome et al. 2002). In Africa, elephants are apparently attracted to recent controlled burns,
10 killing savanna trees that survived the fire (Okello et al. 2008). Although there was significant
11 rabbit and rodent herbivory at our research site, deer browsing was minimal. Oak saplings at
12 sites with significant deer browse pressure might experience comparatively reduced rates of
13 height recovery following prescribed burn.

14 In our study, most of the smaller burned trees changed from single-stemmed saplings to
15 multi-stemmed with a more bushy architecture, and many of the larger saplings had considerable
16 basal sprouting at their bases. It is not clear whether, or at what rate, these multiple coppices
17 might self-prune and recover a single-stemmed architecture. In any case, the increase in fuel
18 loads near the ground associated with these post-burn architectures may put these individuals at
19 increased risk of more severe responses to future fires.

20 Burning to control or reverse forest encroachment into tropical and temperate savanna
21 ecosystems (e.g., Brook & Bowman 2006, Nowacki and Abrams 2008) may encounter similar
22 issues concerning the top-kill and survival of desirable woody species (Wolf 2006).

23

24 **IMPLICATIONS FOR PRACTICE**

- 1 • Valley oak saplings appear able to survive and to recover in height from damage
2 associated with one-time prescribed fires in the spring and early summer. This suggests
3 that spring and early summer burning may be a viable management tool for controlling
4 annual grass or star thistle understories in restored valley oak communities.
- 5 • Managers should consider the temporary setbacks associated with top-kill, including
6 potential changes in architecture of saplings.
- 7 • Land managers may be able to mitigate some of these changes/setbacks by:
- 8 ○ 1) not burning valley oak saplings that are under 300cm tall,
9 ○ 2) conducting burns during the spring when ambient temperatures are lower and
10 when relative humidity and fuel moisture is higher, and
11 ○ 3) reducing understory biomass around sapling oaks via weed control practices.
12 The latter is current practice at several local sites, based in part on this study
13 (Mitch Sears, Jeremiah Mann, pers. comms.).
- 14 • Repeated burning or **intense ungulate** herbivory **in the first few years after burning** are
15 likely to impair recovery of top-killed oaks. Managers are encouraged to **consider** these
16 factors in their restoration prescription, and are encouraged to document **their** results to
17 better understand impacts of browsing and repeat burns. Further research on these
18 effects, including potentially interactive effects on trees and understory biomass, is
19 needed to more fully evaluate fire management as a tool in newly-restored valley oak
20 woodlands.

21

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1 **REFERENCES**

- 2 Allen-Diaz B.H., and J.W. Bartolome. 1992. Survival of *Quercus douglasii* (Fagaceae) seedlings
3 under the influence of grazing and fire. *Madroño* **39**:47-53.
- 4 Alvarado-Sosa, P., A. Blanco-Garcia, and R. Lindig-Cisneros. 2007. Test of alternative nursery
5 propagation conditions for *Lupinus elegans* Kunth plants, and effects on field survival.
6 *Revista Fitotecnia Mexicana* **30**:201-204.
- 7 Arthur, M.A., R.D. Paratley, and B.A. Blankenship. 1998. Single and repeated fires affect
8 survival and regeneration of woody herbaceous species in an oak-pine forest. *Journal of the*
9 *Torrey Botanical Society* **125**: 225-236.
- 10 Barbour, M.G., and R.A. Minnich. 2000. Californian Upland Forests and Woodlands. Pages 161-
11 202 in M.G. Barbour and W.D. Billings, editors. *North American terrestrial vegetation*. 2nd
12 edition. Cambridge University Press, Cambridge, United Kingdom.
- 13 Bartolome, J.W., J.P. McClaran, B.H. Allen-Diaz, J. Dunne, L.D. Ford, R.B. Standiford, N.K.
14 McDougald, L.C. Forero. 2002. Effects of fire and browsing on regeneration of blue oak.
15 Pages 281-286 in R.B. Standiford, D. McCreary, and K.L. Purcell, editors. *Proceedings of*
16 *the fifth symposium on oak woodlands: Oaks in California's changing landscape*; 2001
17 October 22-25. USDA Forest Service General Technical Report PSW-GTR-184. Pacific
18 Southwest Research Station, Forest Service, U.S. Department of Agriculture, Albany, CA.
- 19 Benayas J.M.R, and A. Camacho-Cruz. 2004. Performance of *Quercus ilex* saplings planted in
20 abandoned Mediterranean cropland after long-term interruption of their management. *Forest*
21 *Ecology and Management* **194**:223-233.
- 22 Biswell, H.H. 1989. *Prescribed burning in California wildlands vegetation management*.
23 University of California Press, Berkeley, CA.
- 24 Bolsinger, C.L. 1988. *The hardwoods of California timberlands, woodlands, and savannas*.

- 1 USDA, Forest Serv. Resource Bull. PNW RB-148.
- 2 Bossard, C.C., J.M. Randall, M.C. Hoshovsky. 2000. Invasive plants of California's wildlands.
3 University of California Press, Berkeley, CA.
- 4 Brook, B.W., and D. Bowman. 2006. Postcards from the past: charting the landscape-scale
5 conversion of tropical Australian savanna to closed forest during the 20th century. *Landscape*
6 *Ecology* **21**:1253-1266.
- 7 Brose P.H., and D.H. Van Lear. 1998. Responses of hardwood advance regeneration to seasonal
8 prescribed fires in oak-dominated shelterwood stands. *Canadian Journal of Forest Research*
9 **28**:331-339.
- 10 Cione, N.K., P.E. Padgett, and E.B. Allen. 2002. Restoration of a native shrubland impacted by
11 exotic grasses, frequent fire, and nitrogen deposition in southern California. *Restoration*
12 *Ecology* **10**:376-384.
- 13 Dagit, R. 2002. Post-fire monitoring of coast live oaks (*Quercus agrifolia*) burned in the 1993
14 Old Topanga Fire. Pages 243-249 in R.B. Standiford, D. McCreary, and K.L. Purcell,
15 technical coordinators. Proceedings of the fifth symposium on oak woodlands: Oaks in
16 California's changing landscape; 2001 October 22-25. USDA Forest Service General
17 Technical Report PSW-GTR-184. Pacific Southwest Research Station, Forest Service, U.S.
18 Department of Agriculture, Albany, CA.
- 19 DeBano, L.F., D.G. Neary, and P.F. Folliott. 1998. Fire's effects on ecosystems. John Wiley and
20 Sons, Inc., New York.
- 21 Dey, D.C., and G. Hartman. 2005. Returning fire to Ozark Highland forest ecosystems: effects
22 on advance regeneration. *Forest Ecology and Management* **217**:37-53.
- 23 DiTomaso, J.M., M.L. Brooks, E.B. Allen, R. Minnich, P.M. Rice, and G.B. Kyser. 2006.
24 Control of invasive weeds with prescribed burning. *Weed Technology* **20**:535-548.

- 1 Ferguson, E.R.1957. Stem-kill and sprouting following prescribed fires in a pine-hardwood stand
2 in Texas. *Journal of Forestry* **55**:426-429.
- 3 Fry, D.L. 2008. Prescribed fire effects on deciduous oak woodland stand structure, Northern
4 Idaho Range, California. *Rangeland Ecology & Management* **61**:294-301.
- 5 Gignoux, J., J. Clobert, and J.-C. Menaut. 1997. Alternative fire resistance strategies in savanna
6 trees. *Oecologia* **110**:576-583.
- 7 Greenlee, J.M., and J.H. Langenheim. 1990. Historic fire regimes and their relation to vegetation
8 patterns in the Monterey bay area of California. *American Midland Naturalist* **124**:239-253.
- 9 Griffin, J.R. 1980. Sprouting in fire-damaged valley oaks, Chews Ridge, California. Pages 216-
10 219 in T.R. Plumb, technical coordinator. Proceedings of the symposium on the ecology,
11 management and utilization of California oaks; 1979 June 26-28. USDA Forest Service
12 General Technical Report PSW-144. Pacific Southwest Forest and Range Experiment
13 Station, Forest Service, U.S. Department of Agriculture, Berkeley, CA.
- 14 Haggerty, P.K. 1994. Damage and recovery in southern Sierra Nevada foothill oak woodland
15 after a severe ground fire. *Madroño* **41**:185-198.
- 16 Hare, R.C. 1965. Contribution of bark to fire resistance. *Journal of Forestry* **63**: 248-251.
- 17 Hobbs, T., and T.P. Young. 2001. Growing valley oak. *Ecological Restoration* **19**:165-171.
- 18 Hoffmann, W.A., and O. T. Solbrig. 2003. The role of topkill in the differential response of
19 savanna woody plants to fire. *Forest Ecology & Management* **180**:273-286.
- 20 Holmes, KA., K.E. Veblen, T.P Young, and A.M. Berry. In press. California oaks and fire: a
21 review and case study. Proceedings of the sixth symposium on oak woodlands: Today's
22 challenges, tomorrow's opportunities, October 9-12, 2006, Rhonert Park, Calif. USDA
23 Forest Service General Technical Report. Pacific Southwest Research Station, Forest
24 Service, U.S. Department of Agriculture, Albany, CA.

- 1 Horney, M., R.B. Standiford, D. McCreary, J. Tecklin, and R. Richards. 2002. Effects of wildfire
2 on blue oak in the Northern Sacramento Valley. Pages 261-267 in R.B. Standiford, D.
3 McCreary, and K.L. Purcell, technical coordinators. Proceedings of the fifth symposium on
4 oak woodlands: Oaks in California's changing landscape; 2001 October 22-25. USDA Forest
5 Service General Technical Report PSW-GTR-184. Pacific Southwest Research Station,
6 Forest Service, U.S. Department of Agriculture, Albany, CA.
- 7 Hutchinson, T.F., E.K. Sutherland, and D.A. Yaussy. 2005. Effects of repeated prescribed fires
8 on the structure, composition and regeneration of mixed-oak forests in Ohio. *Forest Ecology
9 and Management* **218**:210-228.
- 10 Katibah, E.F. 1984. A brief history of riparian forests in the Central Valley of California. Pages
11 23-29 in Warner, R.E. and K.M. Hendrix, editors. *California Riparian Systems: Ecology,
12 Conservation, and Productive Management*. University of California Press, Berkeley, CA.
- 13 Kauffman J.B., and R.E. Martin. 1987. Effects of fire and fire suppression on mortality and mode
14 of reproduction of California black oak (*Quercus kelloggii* Newb.). Pages 122-126 in T.R.
15 Plumb and M.N. Pillsbury, technical coordinators. Proceedings of the symposium on
16 multiple-use management of California's hardwood resources; 1986 November 12-14;
17 USDA Forest Service General Technical Report PSW-100. Pacific Southwest Forest and
18 Range Experiment Station, Forest Service, U.S. Department of Agriculture, Berkeley, CA.
- 19 Lulow, M.E., T.P. Young, J.L. Wirka, and J.H. Anderson. Variation in the initial success of
20 seeded native bunchgrasses in the rangeland foothills of Yolo County, California. *Ecological
21 Restoration* **25**:20-28.
- 22 McClaran, M.P., and J.W. Bartolome. 1989. Fire-related recruitment in stagnant *Quercus*
23 *douglasii* populations. *Canadian Journal of Forest Research* **19**:580-585.
- 24 McCarty, K. 1998. Landscape-scale restoration in Missouri savannas and woodlands. *Restoration*

- 1 & Management Notes **16**:22-32.
- 2 Midoko-Iponga, D., C.B. Krug, and S.J. Milton. 2005. Competition and herbivory influence
3 growth and survival of shrubs on old fields: Implications for restoration of renosterveld
4 shrubland. Journal Of Vegetation Science **16**:685-692.
- 5 Nowacki, G.J, and M.D. Abrams. 2008. The demise of fire and "Mesophication" of forests in the
6 eastern United States. Bioscience **58**:123-138.
- 7 Okello, B.D., T.P. Young, C. Riginos, D. Kelly & T. O'Connor. 2008. Short-term survival and
8 long-term mortality of *Acacia drepanolobium* after a controlled burn in Laikipia, Kenya.
9 African Journal of Ecology **46**:395-401.
- 10 Pausas, J.G., C. Blade, A. Valdecantos, J.P. Seva, D. Fuentes, J.A. Alloza, A. Vilagrosa, S.
11 Bautista, J. Cortina, and R. Vallejo. 2004. Pines and oaks in the restoration of Mediterranean
12 landscapes of Spain: New perspectives for an old practice - a review. Plant Ecology **171**:209-
13 220.
- 14 Pavlik, B.M., P.C. Muick, S. Johnson, and M. Popper. 1991. Oaks of California. Cachuma Press,
15 Inc, Los Olivos, CA.
- 16 Paysen, T.E., and M.G. Narog. 1993. Tree mortality six years after burning a thinned *Quercus*
17 *chrysolepis* stand. Canadian Journal of Forest Research **23**:2236-2241.
- 18 Peterson, D.W. and P.B. Reich. 2001. Prescribed fire in oak savanna: fire frequency effects on
19 stand structure and dynamics. Ecological Applications **11**:914-927.
- 20 Plumb, T.R. 1980. Response of oaks to fire. Pages 202-215 in T.R. Plumb, technical coordinator.
21 Proceedings of the symposium on the ecology, management and utilization of California
22 oaks; 1979 June 26-28. USDA Forest Service General Technical Report PSW-144. Pacific
23 Southwest Forest and Range Experiment Station, Forest Service, U.S. Department of
24 Agriculture, Berkeley, CA.

- 1 Regan, A.C., and J.K. Agee. 2004. Oak community and seedling response to fire at Fort Lewis,
2 Washington. *Northwest Science* **78**:1-11.
- 3 Sanchez-Gomez, D., F. Valladares, and M.A. Zavala. 2006. Performance of seedlings of
4 Mediterranean woody species under experimental gradients of irradiance and water
5 availability: trade-offs and evidence for niche differentiation. *New Phytologist* **170**:795-805.
- 6 Schwan, J., H. Fong, and H.K. Hug. 1997. Wildfire and oak regeneration at the urban fringe.
7 Pages 559-564 in N.H. Pillsbury, J. Verner and W.D. Tietje, technical coordinators.
8 Proceedings of a symposium on oak woodlands: ecology, management, and urban interface
9 issues; 1996 March 19-22; San Luis Obispo, CA. USDA Forest Service General Technical
10 Report PSW-GTR-160. Pacific Southwest Research Station, Forest Service, U.S. Department
11 of Agriculture, Berkeley, CA.
- 12 Stromberg, M., T.P. Young, J. Wirka, and P. Kephart. 2007. California Grassland Restoration.
13 Pages 254-280 in: Stromberg, M., J.D. Corbin, and C.M. D'Antonio, editors. *Ecology and
14 Management of California Grasslands*. University of California Press, Berkeley, CA.
- 15 Swiecki, T.J., and E. Bernhardt. 1998. Effects of fire on naturally occurring blue oak (*Quercus*
16 *douglasii*) saplings and planted valley oak (*Q. lobata*). Seventh workshop on seedling
17 physiology and growth problems in oak plantings; 1998 September 27-29; South Lake
18 Tahoe, CA. North Central Research Station, Forest Service, U.S. Department of Agriculture.
- 19 Swiecki, T.J., and E. Bernhardt. 2002. Effects of fire on naturally occurring blue oak (*Quercus*
20 *douglasii*) saplings. Pages 251-259 in R.B. Standiford, D. McCreary, and K.L. Purcell,
21 technical coordinators. Proceedings of the fifth symposium on oak woodlands: Oaks in
22 California's changing landscape; 2001 October 22-25. USDA Forest Service General
23 Technical Report PSW-GTR-184. Pacific Southwest Research Station, Forest Service, U.S.
24 Department of Agriculture, Albany, CA.

- 1 Tabachnick, B.G., and L.S. Fidell. 2001. Using multivariate statistics, fourth edition. Allyn and
2 Bacon, Boston.
- 3 Tietje, W.D., J.K. Vreeland, and W.H. Weitkamp. 2001. Live oak saplings survive prescribed
4 fire and sprout. *California Agriculture* **55**:18-22.
- 5 Vaghti, M.G., and S.E. Greco. 2007. Riparian vegetation of the Great Valley. Pages 425-455 in
6 Barbour, M.G., T. Keeler-Wolf and A. Schoenherr, editors. *Terrestrial Vegetation of*
7 *California*, 2nd ed., University of California Press, Berkeley, CA.
- 8 Van Mantgem, P., M. Schwartz and M. Keifer. 2001. Monitoring fire effects for managed burns
9 and wildfires: coming to terms with pseudoreplication. *Natural Areas Journal* **21**:266-273.
- 10 Whelan, R.J. 1995. *The ecology of fire*. Cambridge University Press, Cambridge, Great Britain.
- 11 Wills, R. 2006. Central Valley Bioregion. Pages 295-320 in Sugihara, N.G. et al., editors. *Fire in*
12 *California's ecosystems*, University of California Press, Berkeley, CA.
- 13 Wolf, J. 2006. Effects of disturbance frequency on canopy age structure and species composition
14 in a managed midwestern oak savanna. *Physical Geography* **27**:519-533.
- 15 Young, T.P., and R.Y. Evans. 2001. Container stock versus direct seeding for woody species in
16 restoration sites. *Comb. Proc. Intl. Plant Propagation Soc.* (2000) **50**:577-582.
- 17 Young, T.P., and R.Y. Evans. 2005. Growth and survivorship of valley oaks (*Quercus lobata*)
18 planted from seed and containers. *Native Plants Journal* **6**:83-90.
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1

2 Tables:

3

4 **Table 1-** Comparison of proportions of *Q. lobata* saplings that exhibited different fire responses,
 5 and the mean number of basal sprouts per tree (\pm one s.e.), by burn treatment, treating the eight
 6 or nine fire blocks per treatment as replicates. Responses significantly different (ANOVA,
 7 Tukey's HSD) within each fate class are denoted by different letters.

8

Treatment	Dead	Main leader dead, basal sprouting	Main leader alive	# basal sprouts	Total # trees
Control	0.00 \pm 0.00 a	0.00 \pm 0.00 a	1.00 \pm 0.00 a	0.8 \pm 0.1 a	93
Summer03 burn	0.03 \pm 0.02 a	0.72 \pm 0.09 b	0.25 \pm 0.09 b	4.6 \pm 0.5 b	88
Spring04 burn	0.04 \pm 0.02 a	0.66 \pm 0.06 b	0.30 \pm 0.07 b	4.6 \pm 0.3 b	94

9

10 **Table 2-** Multiple logistic regression of preburn height, understory biomass and fire
 11 temperature as predictors of severity of *Q. lobata* sapling response to prescribed fire
 12 (death or top-kill versus leader alive), using individual tree measurements as
 13 replicates.

Predictive factors	Burn treatment	χ^2	p-value	McFadden's ρ^2
Multivariate combination of all three factors	Summer03	18.4	0.0004	0.36
	Spring04	69.0	<0.0001	0.63
Tree height	Summer03	13.0	0.0003	
	Spring04	51.4	<0.0001	
Fire temperature	Summer03	4.3	0.04	
	Spring04	9.2	0.002	
Understory biomass	Summer03	3.8	0.05	
	Spring04	2.4	0.12	

14

1 **Figure Captions:**

2

3 **Figure 2-** Proportions of *Q. lobata* saplings of different heights that

4 exhibited different fire responses in the Summer03 burn treatment. Sample

5 sizes (shown above height classes) are the numbers of individual trees in

6 each height class.

7

8 **Figure 3-** Proportions of *Q. lobata* saplings of different heights that

9 exhibited different fire responses in the Spring04 burn treatment. Sample

10 sizes (shown above height classes) are the numbers of individual trees in

11 each height class.

12

13 **Figure 1-** Mean height of *Q. lobata* saplings over a 3.5 year period by burn

14 treatment: unburned control, Summer03 prescribed burn, and Spring04

15 prescribed burn. Analysis is by burn treatment, treating the eight or nine fire

16 blocks per treatment as replicates. Error bar denotes one standard error.

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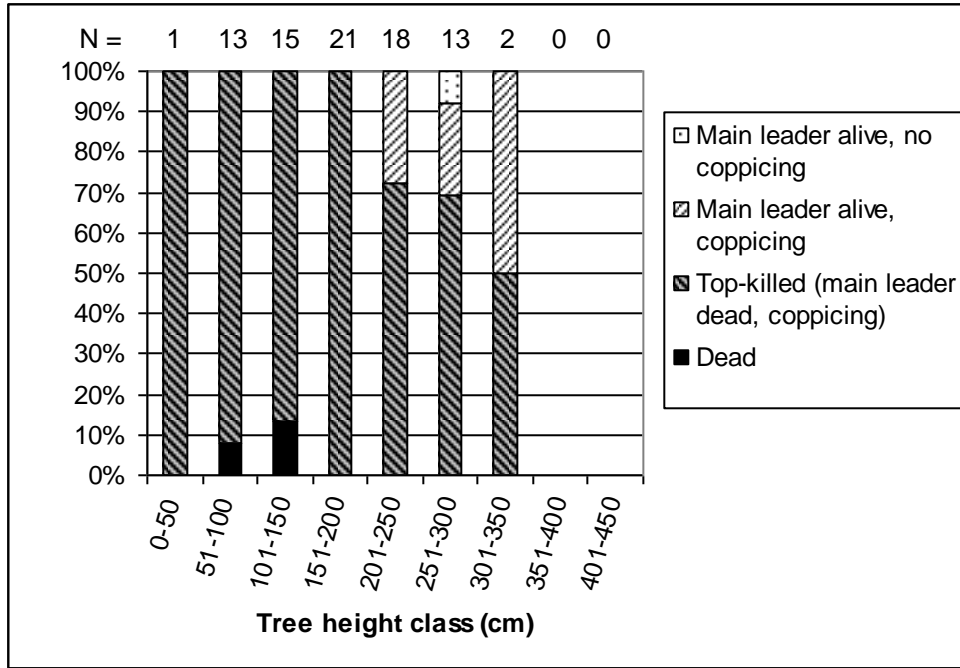


Figure 2

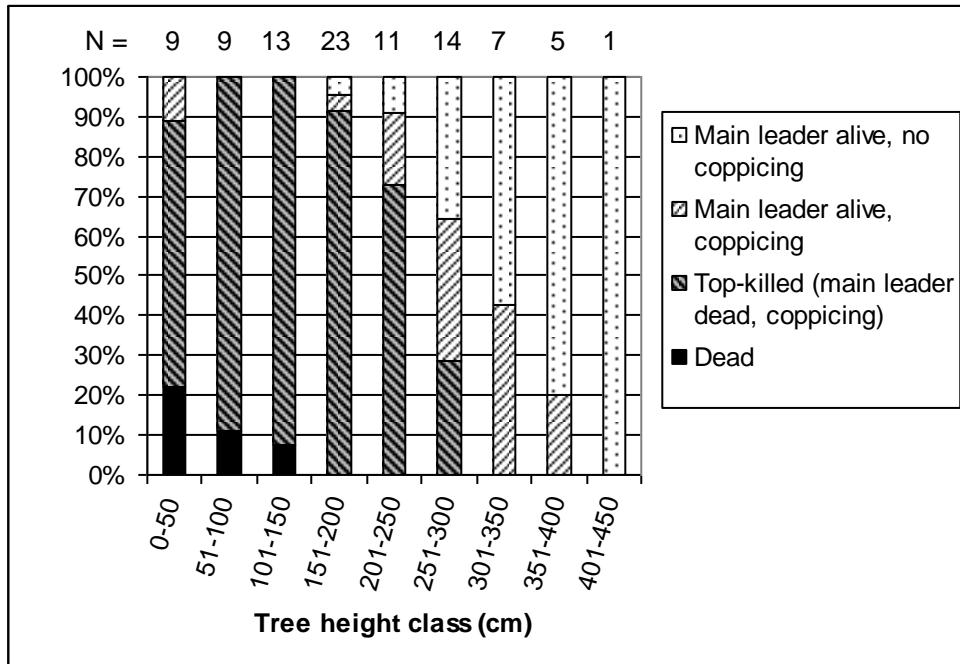
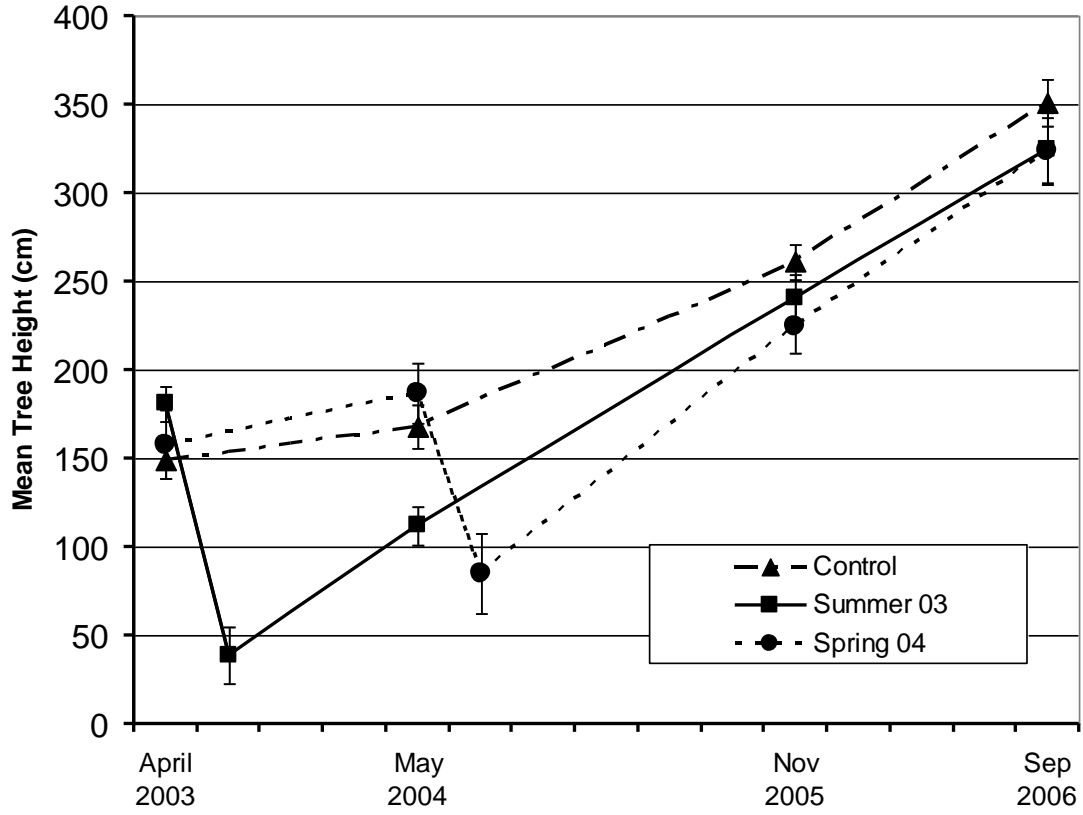


Figure 3

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Figure 1