Population Densities and Tree Diameter Effects Associated With Verbenone Treatments to Reduce Mountain Pine Beetle-Caused Mortality of Lodgepole Pine

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ABSTRACT Mountain pine beetle, *Dendroctonus ponderosae* Hopkins (Coleoptera: Curculionidae: Scolytinae), is among the primary causes of mature lodgepole pine, *Pinus contorta* variety *latifolia* mortality. Verbenone is the only antiaggregant semiochemical commercially available for reducing mountain pine beetle infestation of lodgepole pine. The success of verbenone treatments has varied greatly in previous studies because of differences in study duration, beetle population size, tree size, or other factors. To determine the ability of verbenone to protect lodgepole pine over long-term mountain pine beetle outbreaks, we applied verbenone treatments annually for 3 to 7 yr at five western United States sites. At one site, an outbreak did not develop; at two sites, verbenone reduced lodgepole pine mortality in medium and large diameter at breast height trees, and at the remaining two sites verbenone was ineffective at reducing beetle infestation. Verbenone reduced mountain pine beetle infestation of lodgepole pine trees in treated areas when populations built gradually or when outbreaks in surrounding untreated forests were of moderate severity. Verbenone did not protect trees when mountain pine beetle populations rapidly increase.

KEY WORDS mountain pine beetle, verbenone, semiochemical, lodgepole pine, antiaggregant

Mountain pine beetle, *Dendroctonus ponderosae* Hopkins (Coleoptera: Curculionidae: Scolytinae) is one of the most damaging forest insects in North America (Furniss and Carolin 1977). Tree losses from beetle infestation have exceeded millions of trees a year in some western states, with impacts on timber values and ecosystem functions. Mountain pine beetle-caused tree mortality contributes to increases in fuel loads that can influence fire behavior (Klutsch et al. 2011) and cause safety concerns in recreation areas, roadways, and power line right of ways associated with the imminent fall of dead trees. Additionally, it negatively affects timber, esthetic values, water quality, and fish and wildlife habitat (Fettig et al. 2007). In many areas of western North America, lodgepole pine, *Pinus contorta* variety *latifolia* Engelmann is the principal host for mountain pine beetle. During outbreaks, 70–90% of lodgepole pine measuring ≥23 cm in diameter, DBH (1.4 m above the ground or breast height) can be killed over vast areas (Safranyik et al. 1974, Amman 1977, Klein et al. 1978, Progar 2005, Klutsch et al. 2009, Westfall and Ebata 2011, Kashian et al. 2011). Sufficient numbers of lodgepole pine trees increase to susceptible diameters every 20–40 yr, rendering stands vulnerable to mountain pine beetle outbreaks (Amman and Schmitz 1988; Parker and Stipe 1995; Alfaro et al. 2004; Axelson et al. 2009, 2010; Hrinkevich and Lewis 2011).

Mountain pine beetle prefer to infest large diameter trees (Klein et al. 1978, Cole and Amman 1980, Amman and Cole 1983, Björklund and Lindgren 2009), perhaps because the thicker bark protects their offspring against low winter temperatures (Cole 1975, 1981). The thicker bark also protects beetle larvae from the parasitic wasp *Coeloides dendroctoni* Cushman (Hymenoptera: Braconidae), which has a relatively short ovipositor (Reid 1963, Cole 1981). Additionally, large trees tend to produce thicker phloem that provides more resources and this is believed to foster beetle survival (Amman 1969, 1975; Klein et al. 1978; Graf et al. 2012). However, survival and net brood production are higher in large trees, even when large trees have thin phloem (Reid 1963), possibly because beetle infestation occurs at greater heights and large trees simply have greater surface areas (Björklund et al. 2009).

Cole and Amman (1980), Mitchell and Preisler (1991), and Safranyik and Carroll (2006) suggest large

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Table 1. Location of sites in the western United States used to test verbenone as a treatment for deterring mountain pine beetle (*Dendroctonus ponderosae*) infestation of lodgepole pine (*Pinus contorta* var *latifolia*)

Location	Latitude	Longitude	Plot size (ha)	Lodgepole pine basal area (m^2/ha)	Sanitation	Verbenone (grams per pouch)	Verbenone (pouches per plot)	Treatment period
Bellaire Lake, CO	40.7719	−105.6222	0.4	29	Yes	7.0	40	2009–2011
Redfish Lake, ID	44.1221	−114.9411	0.2	21	No	5.0	20	2000–2004
Stanley Lake, ID	44.2903	−115.0745	0.4	22	No	7.0	20	2005–2011
Heber, UT	40.6368	−110.9440	0.4	14	No	7.0	20	2005–2011
Alpine, WY	43.1692	−111.0029	0.4	22	Yes	7.0	40	2009–2011

diameter lodgepole pines are necessary for mountain pine beetle outbreaks to occur because they attract pioneer beetles into the stand, and Preisler and Mitchell (1993) indicate that beetle population growth is only possible while large trees remain in the stand. According to Cole and Amman (1980), outbreaks require trees 35.6 cm and larger DBH to increase in severity or maintain the previous year's level. Smaller trees may account for more than half the trees killed during an outbreak, but they seem to be unimportant for maintaining an outbreak (Klein et al. 1978).

Verbenone (4,5,5-trimethylbicyclo [3.1.1] hept-3-en-2-one) is the most effective olfactory stimulant for disrupting beetle infestation, and there are commercially available synthetic formulations of this semiochemical (Gillette and Munson 2009). Managers have been attempting to use verbenone to disrupt mountain pine beetle from infesting large trees occurring in campgrounds, parks, and other high value areas used by the public for their esthetic value. In nature, the majority of verbenone is produced by gut microorganisms and symbiotic yeasts associated with the beetles (Leufvén et al. 1984; Borden et al. 1987, 2007; Hunt and Borden 1989). Verbenone is considered an indicator of declining host tissue quality and its quantity is a function of the extent of microbial degradation (Lindgren et al. 1996). Results from a number of studies suggest verbenone can prevent mountain pine beetle infestation for a single year. Point estimates of percent mortality in control versus verbenone treatments from some single-year experiments are 24.4 versus 7.4% (Amman et al. 1989), 21.3 versus 11.4% (Lindgren et al. 1989), 21 versus 2%, 15 versus 1% (Bentz et al. 2005). These studies were single year experiments, therefore, it is unknown if verbenone can provide continued protection of lodgepole pines over the duration of beetle outbreaks. The long-term efficacy of verbenone treatments is questionable because mountain pine beetle's response to verbenone may diminish in treated areas after mountain pine beetles have reduced the availability of suitable host trees elsewhere. Thus, short-term studies conducted during the early stages of an outbreak could overvalue verbenone as a treatment for protecting lodgepole pine from infestation by mountain pine beetle because they are frequently conducted when beetle population levels are low and there are many large diameter host trees available. Only Progar (2003, 2005) has evaluated the effect of verbenone treatments on mountain pine beetle in lodgepole pine stands on the same plots for successive years. Point estimates from this study suggest repeated verbenone treatment reduced beetle-caused tree mortality from an average of 75–57% over a 5 yr period, but this difference was not statistically significant. Clearly more expansive studies are needed to determine if verbenone can protect large trees throughout an outbreak. In this study, verbenone efficacy was assessed in multi-year experiments conducted at five sites distributed throughout the western United States.

Most verbenone studies have considered all tree size classes collectively, so little is known about the ability of verbenone to specifically protect the large trees preferred by beetles. This is important because it is the large trees that are usually most valued by resource managers. This study had two objectives. The first objective was to determine if verbenone efficacy varied across tree size classes, and the second objective was to determine if verbenone can provide multiple year protection from mountain pine beetle until outbreaks subside.

Materials and Methods

Verbenone treatments were established in the same plots from 3 to 7 yr at various experimental sites (Table 1; Fig. 1). Each site was comprised of six verbenone-treated and six untreated plots. Plots were spaced at least 200 m apart, and treatments were randomly assigned to plots. The plots were established in lodgepole pine stands when mountain pine beetle populations were thought to be increasing toward outbreak levels. In the 2 yr before plot establishment, beetle-caused tree mortality had been <15% in all plots.

Pouches containing 5 g of verbenone (Contech International Inc., Delta, British Columbia, Canada) were deployed at the Redfish Lake, ID, site, 7 g of verbenone (Synergy Semiochemicals Inc., Burnaby, British Columbia, Canada) were used at all other sites. All pouches were composed of 98% verbenone (80%-(−)20%(+)) calibrated to release verbenone at ≈25 mg/d at 20°C and were affixed to the north side of lodgepole pines 4 m above the ground during the third week of June in each study year in a grid pattern at ≈10 or 20 m intervals (Table 1). Beetle-killed trees were removed annually from verbenone treated plots at two sites (Table 1).

The DBH of all live trees in each plot were recorded at the beginning of the study. Thereafter, the DBH of all trees killed by mountain pine beetle were measured each fall. A tree was considered to be killed by beetles if it was surrounded by boring dust; the circumference

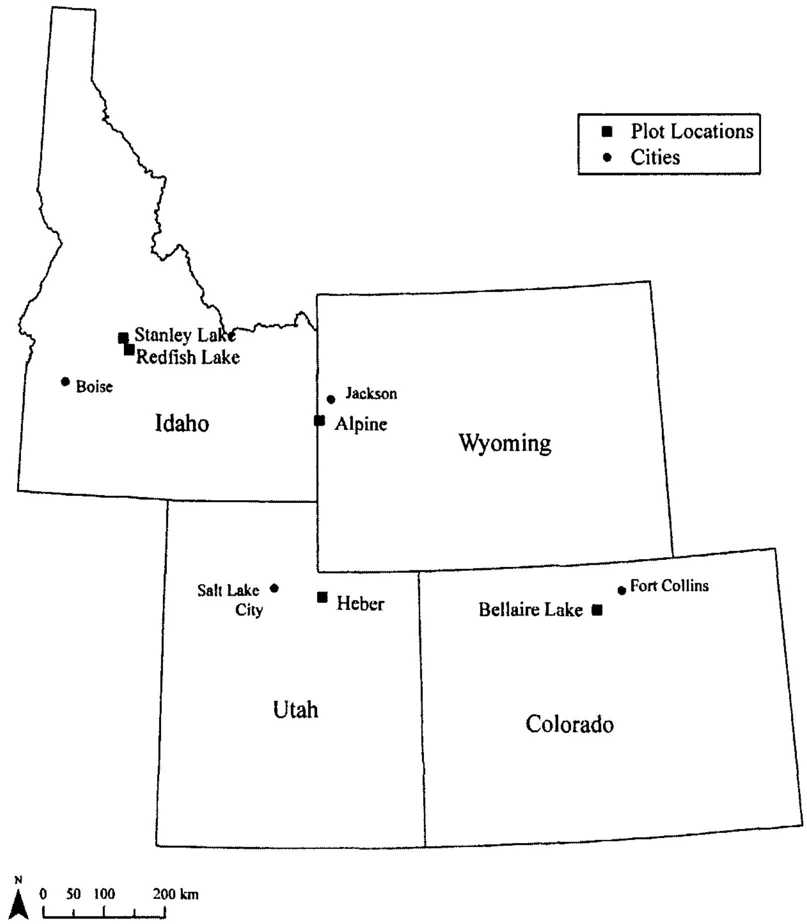

Fig. 1. Map of study locations in the western United States.

of the bole was covered by pitch tubes over galleries that contained beetle broods; and/or the circumference of the bole was covered in pitch tubes and the needles were fading. Verbenone treatment and data collection occurred for the duration of an outbreak at Redfish Lake, ID, Stanley Lake, ID, and Heber, UT, while the study sites at Bellaire Lakes, CO, and Alpine, WY, were monitored for 3 yr.

Tree diameters were partitioned into three classes for analysis: small (<23 cm DBH), medium (23–33 cm DBH), and large (>33 cm DBH). Zeros prevented the data from following a standard probability distribution, so the analysis was based on bootstrap confidence intervals (Hjorth 1994). Computing these intervals entailed calculating the ratio of killed trees to total trees in each of the three size classes in each plot. Then, for each combination of site and treatment, six of these ratio observations were randomly drawn with replacement and their mean calculated. Random sampling and mean calculations were repeated 5,000 times and then CIs calculated using the percentile method (Dixon 2001).

Results and Discussion

At the beginning of the study, the number of small diameter trees exceeded the number of medium and large diameter trees at all of our sites (Fig. 2). Consistent with previous research, tree mortality point estimates for untreated plots tended to be greater for medium and large trees compared with small trees (Fig. 3) (Amman 1969, Cole and Amman 1969, Mitchell and Priesler 1991, Björklund and Lindgren 2009).

At Heber, UT, point estimates suggest verbenone reduced small, medium, and large tree mortality by 15, 31, and 54%, respectively. All three of these reductions were statistically significant at the 0.95 confidence level (CL) because the CIs for verbenone and the control do not overlap (Fig. 3). Similarly, at Stanley Lake, ID, point estimates for mortality reductions were 8, 30, and 40%, for small, medium, and large trees, respectively. The reduction for medium and large trees was significant at Stanley Lake, ID, even though the CI tails for the large trees overlap somewhat and this is because only 0.025 of the probability appears in the tail of a 95% CI (Fig. 3). The estimates for Heber, UT, and Stanley Lake, ID, indicate that verbenone sometimes protects the large trees that managers are most concerned about. However, data from Redfish Lake, ID, and Bellaire Lakes, CO, illustrates that verbenone does not consistently protect lodgepole pine trees from mountain pine beetle infestation (Fig. 3). Finally, at Alpine, WY, beetles remained at

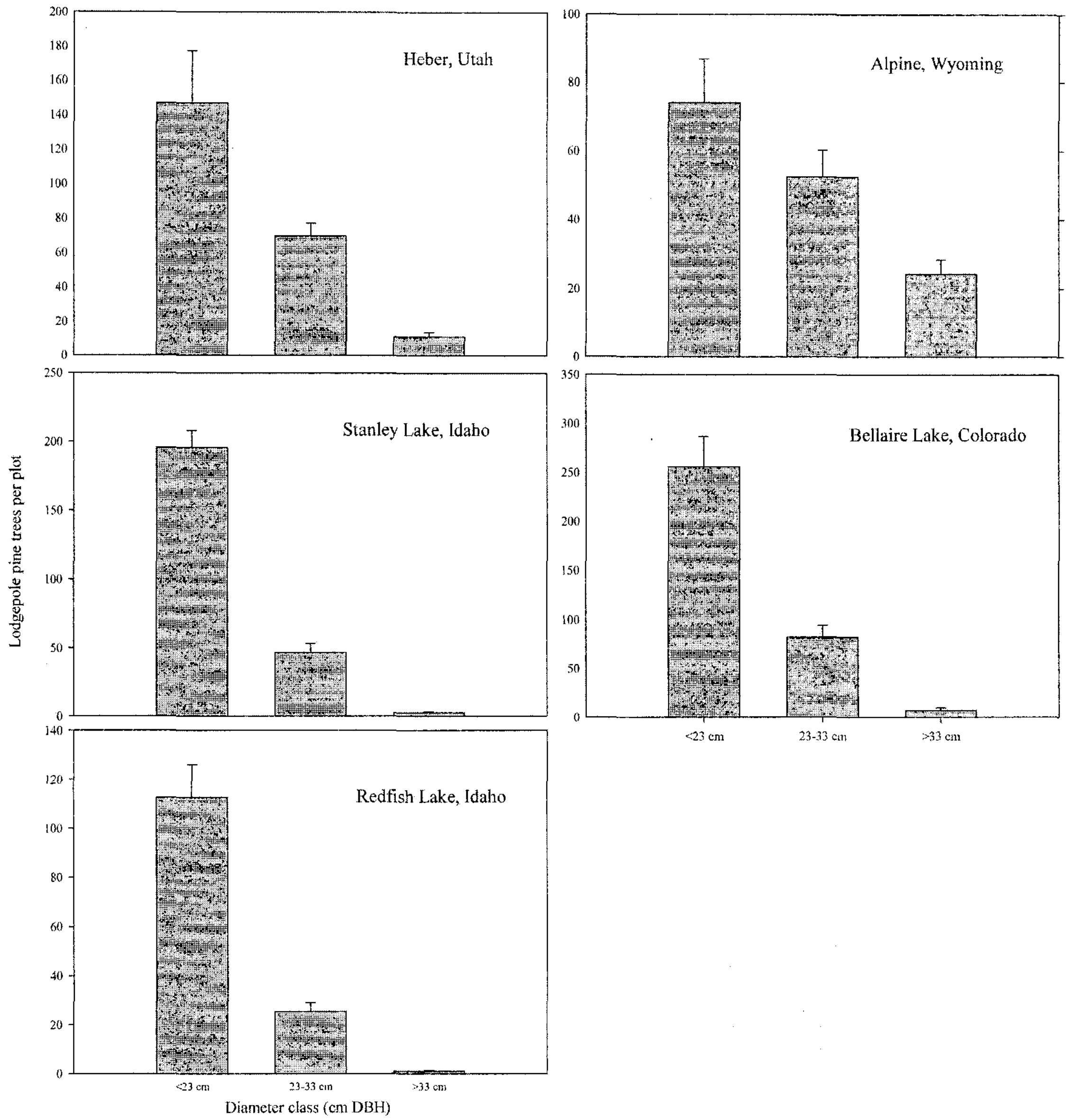

Fig. 2. Average and SE of the number of lodgepole pine trees within each size class (centimeters DBH) at each site before verbenone treatment, at the beginning of the study.

low population levels when data collection for this study ended.

Rapid expansion of mountain pine beetle populations, either through rapid growth, or immigration, appears to be a strong contributing factor of verbenone's inefficiency as a tree protectant. Amman and Lindgren (1995) indicated that large populations of beetles at the peak of an outbreak may not respond to verbenone treatments. Lynch et al. (2006) noted that mountain pine beetle dynamics may differ in an outbreak of low or moderate severity compared with high severity. Verbenone did not significantly reduce tree mortality at our plots at Redfish Lake, ID, and at Bellaire Lake, CO. Each of these sites had rapidly growing beetle populations as indicated by the fast-increasing portion of infested and killed trees during the first 2 yr of the outbreak (Fig. 4). Untreated plots at Redfish Lake, ID, incurred mortality of >50% from 2000 to 2002; Bellaire Lake, CO, untreated plots had mortality of 40% from 2009 to 2010. Bentz et al. (2005) also indicated the verbenone treatment was unsuccessful when ≈60% of the available trees had been infested the previous year. In contrast, the populations at Heber, UT, and Stanley Lake, ID, where verbenone was effective, did not incur more than a 10% increase in beetle-caused mortality in any single year of the study (Fig. 4).

Our data shows a preference by mountain pine beetle for large diameter trees, but at some of our sites the overall portion of large diameter trees was minimal

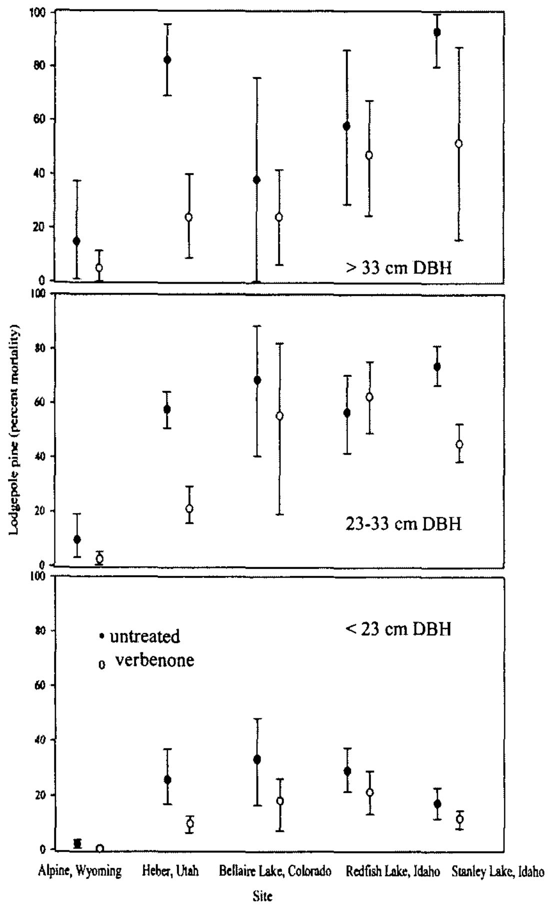

Fig. 3. Point estimates (dots) and 95% CIs (bars) quantifying percent mortality of lodgepole pine caused by mountain pine beetle in control (C) and verbenone-treated (V) plots in three size classes at five sites in the western United States.

(Fig. 2), yet the sites maintained rapidly growing beetle populations. Plots at Redfish Lake, ID, and Bellaire Lakes, CO, had relatively low numbers of large trees present, but experienced 40–50% mortality in 1 or 2 yr. However, the number or portion of large trees needed to attract mountain pine beetle to an area is not known, nor the level of immigration contributing to these outbreaks.

Reducing stand density by thinning is recommended for mature lodgepole pine stands to reduce susceptibility to beetle infestation (Fettig et al. 2007). Basal area of our study sites ranged from 14 m^2/ha in plots at Heber, UT, to 29 m^2/ha at Bellaire Lake, CO (Table 1). Mature (80–100 yr old) stands usually have a basal area of 30–40 m^2/ha (Cole and Edminster 1984). Many of our study plots were located within and among campgrounds and other recreation areas where fewer trees were present, and comparable to thinned stands, having a basal area in the low 20s m^2/ha (Table 1). The low basal area at Heber, UT, may be contributing to the ability of verbenone to protect trees at this site. The sites at Redfish Lake, ID, and Bellaire Lakes, CO, where verbenone did not protect trees had plots mostly located within and around campgrounds. Bellaire Lakes, CO, had the highest basal area of all of our sites, and that may have been a factor contributing the rapid increase in beetle populations at this site. However, the basal area of the Redfish Lake, ID, plots was only 21 m^2/ha, which should have reduced the attraction of beetles to the area. Additionally, Amman et al. (1988) showed that in a stand that was in the path of an ongoing mountain pine beetle outbreak, density had little effect, with greater spacing between trees not deterring host finding by mountain pine beetle.

Current management practices to reduce beetle-caused tree mortality rely primarily on cutting down and removing infested and susceptible trees (Amman et al. 1991). Because large DBH trees are necessary to initiate a mountain pine beetle outbreak (Safranyik and Carroll 2006) and provide habitat for expanding beetle populations (Cole and Amman 1980), managers should focus management efforts on protecting these larger trees. Concentrating those efforts on large DBH trees may be more cost effective because large trees comprise a small portion of the forest (Fig. 2), and therefore require fewer resources to manage. Albeit, the efficacy of semiochemical tree protection is reduced during rapidly growing mountain pine beetle outbreaks.

More intensive management options are frequently used in recreation sites or administrative areas to reduce the impacts of mountain pine beetle infestation. Insecticidal sprays have been effective for protecting individual high value trees (Hastings et al. 2001, Fettig et al. 2006). However, some recreational areas are too large, and hence too expensive to treat with insecticides or tree removal treatments. This suggests further verbenone research is warranted because it may be a cost-effective tool for protecting lodgepole pine from beetle infestation in some areas. Further research could evaluate higher doses of verbenone or treatments that place verbenone only on the largest trees.

Other ways to improve verbenone efficacy may involve using it in combination with other semiochemicals. Fettig et al. (2005, 2008, 2012) has shown increased verbenone efficacy after combining it with nonhost volatiles (benzyl alcohol, benzaldehyde, *trans*-conophthorin, guaiacol, nonanal, and salicylaldehyde), three green leaf volatiles [(E)-2-hexenal, (E)-2-hexen-1-ol, and (Z)-2-hexen-1-ol], with verbenone to reduce western pine beetle (*Dendroctonus brevicomis* LeConte) attraction to baited traps. Huber et al. (2001) has shown increased tree protection when nonhost volatiles and green-leaf volatiles were added as a supplement to verbenone. Alternative methods of delivering verbenone may also improve its efficacy. Gillette et al. (2006, 2009) has demonstrated the efficacy of verbenone impregnated plastic flakes in reducing mountain pine beetle infestation in ground and aerial applications.

In summary, we found that verbenone did not protect trees at sites where mountain pine beetle densities were increasing rapidly, as indicated by the number of infested trees in a single season, but was more effective