PERFORMANCE AND MORPHOLOGY IN *SEQUOIADENDRON* GENOTYPES OUTSIDE OF THEIR RANGE

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ABSTRACT

PERFORMANCE AND MORPHOLOGY IN *SEQUOIADENDRON* GENOTYPES OUTSIDE OF THEIR RANGE

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In its current fragmented distribution in 75 groves along the western slope of the Sierra Nevada, *Sequoiadendron giganteum* (SEGI) may be vulnerable to extreme shifts in environmental conditions such as warming temperatures and drought stress, which may reduce the already limited habitat for SEGI in native groves. Interest in outplanting of this iconic species for the objectives of genetic conservation and timber utilization due to decay resistance of heartwood would be supported by information on population variation to inform seed collection for these plantings. To that end, I assessed three SEGI common-garden trials which had been planted in spring 1981 at the USDA Forest Service Foresthill Seed Orchard (FSO), north of the current species range and at lower elevation, in summer 2009. My analysis of genetic variances and geographic patterns of variation among populations of SEGI stecklings (rooted cuttings) from a 23 grove sample (trial 1 and 2) revealed higher than expected genetic variances for tree size and form traits. Genetic variance of heartwood decay was low. The area of SEGI native grove origin and the extent of grove isolation were the strongest predictors of tree size at FSO, with the grove samples originating from larger and less isolated native groves growing best. Accounting for the effect of grove area, SEGI grove samples originating from higher

elevation native groves with a history of past harvesting were largest by height. In mixed species plantings of SEGI seedlings and five mixed conifer species co-occurring in SEGI's native range (trial 2 and 3) several mixed conifer species, including *Pinus ponderosa* (PIPO) and *Pinus lambertiana* (PILA) outgrew the SEGI seedlings. In plantings outside of SEGI's native range, SEGI may be outcompeted by mixed conifers such as PIPO, particularly on dry sites at lower elevations.

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1. INTRODUCTION

Understanding the genetic variation of forest tree species is of growing concern to ecologists and land managers faced with unpredictable changes in species habitat and distributions brought on by a rapidly changing climate. Most woody species maintain large amounts of genetic variation within-populations relative to other vascular plant species allowing them to endure environmental stochasticity over their relatively long lifespan (Hamrick and Godt 1989). Expectations for woody species based on life history traits are that tall, long-lived, wind-pollinated species with large ranges will maintain high levels of genetic diversity (Hamrick et al. 1992). Conifer species with endemic or fragmented ranges are expected to possess less genetic diversity and may exhibit more variation among populations (Hamrick et al. 1992).

Sequoiadendron giganteum (SEGI) is a species with contradictory traits when it comes to these expectations of genetic diversity. It is the largest tree by volume, able to attain heights in excess of 90 m, and one of the longest lived conifer species (~3200 years) (Weatherspoon 1990). However, it has a limited, endemic native range and may have endured a population bottleneck reducing its genetic diversity at some point in its long evolutionary history (Fins and Libby 1982). Though it is a tall, wind-pollinated species, the seeds of SEGI have a small wing limiting dispersal distances. The combination of limited native range, limited ability to disperse, and limited genetic diversity may make this species particularly vulnerable to rapid environmental changes in its native range (Aitken et al. 2008, York et al. 2013a).

In addition to its great size and longevity, there is growing interest in planting SEGI on timberlands in California (Kitzmiller and Lunak 2012) due to SEGI's decay resistant heartwood, which is similar in quality to *Sequoia sempervirens* (SESE) (Cockerell et al. 1971, Piirto 1986, Knigge 1993). This potential for timber utilization coupled with its limited genetic resources, makes SEGI a prime candidate for planting outside of its current range for the dual purpose of timber utilization and conservation (Kitzmiller and Lunak 2012). A better understanding of SEGI population genetic variation will help inform seed collection strategies in the native groves to achieve successful outplanting of SEGI to meet these objectives. This knowledge will also aid in the development of conservation and management strategies for the species within its native range.

1.1 Distribution of SEGI and Climate Change

In its native range, SEGI is distributed in 75 disjunct groves in a 420-km stretch not more than 24-km wide along the western slope of the Sierra Nevada averaging 1700 - 2500 m (5000-7500 ft) elevation (Rundel 1969, Harvey et al. 1980, Willard 2000). Occurring between 35° and 39° N, total area of these groves is not more than 14,500 ha (Harvey et al. 1980) and the individual groves vary in size from 1-1620 ha. The smallest and most northern grove, the Placer Grove, contains only six trees and is probably inbred (Hartesveldt et al. 1975' Fins and Libby 1982, Libby 1986). The eight discontinuous northern groves are separated by as much as 90 km and spread over 310 km of the north to south range, though occupying a fraction of total grove area (≤ 600 ha). The central

and southern groves form a more continuous belt within a distance of 110 km with a maximum distance between groves of 7 km (Rundel 1971). The central and southern groves comprise the majority of grove area at over 13,000 ha.

In contrast to this present limited distribution, fossil forms ascribed to the genus *Sequoiadendron* were found throughout present-day western North America and Europe (Axelrod 1959, Hartesveldt et al. 1975, Harvey 1985, Ahuja 2008). It is hypothesized that in response to a decrease in winter low temperatures and summer precipitation during the Pliocene SEGI migrated south and west across the Sierra Nevada before these ranges had risen (geologic uplift) to their present heights two to five million years ago. The changing climate and rise of the Sierra Nevada led to the extinction of the eastern populations. Whether SEGI once existed as a more continuous belt along the western slope of the Sierra Nevada or was always isolated in groves is unknown.

There is evidence in pollen records that SEGI was present in the vicinity of Mono Lake on the east side of the Sierra Nevada as recently as 10,000 - 11,500 years ago, at the end of the last glacial period (Davis 1999). This is far from any current grove location and on the other side of the Sierra crest from all known groves. There is also evidence that SEGI occurred at much lower (Cole 1983, Atwater et al. 1986) and higher elevations (Davis and Moratto 1988, Power 1998) in the vicinity of current native grove locations, likely in response to glacial shifts > 10,000 years ago. Over the last 5,000 years, percent of SEGI pollen at seven sites in the central and south-central Sierra Nevada has increased in abundance most above 2,000 m (Anderson and Smith 1994). In a site currently

occupied by SEGI, Log Meadow within Giant Forest, pollen records indicated that SEGI was absent until approximately 4,500 years ago (Anderson 1994).

In its current fragmented distribution, SEGI could be vulnerable to extreme shifts in environmental conditions. Though past studies have indicated that SEGI grove boundaries have been stable in size for the last 500-1,000 years (Rundle 1972, Stephenson 1994), increased tree mortality is predicted throughout the western United States due to a rapidly warming climate and increasing drought stress in the Sierra Nevada (van Mantgem et al. 2009). Though there is historic data indicating that SEGI has expanded and contracted its range since the last glacial maximum in response to climate shifts (Harvey 1986, Millar and Woolfenden 1999), it is unlikely that during this current period of climate change SEGI will have time to migrate to safe sites (Aitken et al. 2008 York et al. 2013a).

1.2 Genetic Variation in SEGI Traits

To endure a variety of environmental conditions spanning millennia, a long-lived species such as SEGI is expected to possess a great amount of genetic variation (Hamrick et al.1992). From previous studies it is clear that this is not the case for SEGI (Libby 1986). With a genome size of 9,700 million base pairs (MB), it is less diverse than most gymnosperms and far less diverse than the closely related *Sequoia sempervirens* (SESE), which has a genome size of 31,500 MB (Ahuja 2008). In the first published study on genetic variability in SEGI, substantial differences were found between northern and southern populations in nursery propagules from the seed collection that established the

FSO trials (Fins and Libby 1982). It was determined that there was little to no gene flow between the northern and southern populations. Isozyme variability, tested using starch gel electrophoresis, revealed a north to south trend of increasing heterozygosity, an indicator of genetic variation. However, the relationship of latitude, longitude, and elevation of sampled SEGI native-groves to SEGI tree size and form traits was generally weak with the exception of the northernmost and southernmost grove samples (Fins and Libby 1982, Libby 1986).

The northernmost Placer Grove is thought to be inbred with only six large living trees in the native grove. Its propagules have demonstrated consistently poor performance in provenance trials (Fins and Libby 1982). Though genetic variation by heterozygosity tended to increase with decreasing latitude, the southernmost Deer Creek propagules have also demonstrated consistently poor performance in provenance trials. Deer Creek Grove, with 30 large, living trees, has a small native population, but evidence strongly suggested that inbreeding was not occurring within this grove (Fins and Libby 1982).

In Europe, SEGI has been planted between 39° - 61° N, north of the current latitude range in California. In several of these studies, SEGI performance has been related to native-grove geographic characteristics. In these experiments planted north of the current range in Europe, SEGI from northern populations were expected to perform best. However, in these common-garden trials, best performance was found in SEGI originating from central and southern populations (Dekker-Robertson and Svolba 1991). Overall, though, strong trends relating growth to latitude of native grove origin were not detected in these European studies. Stronger, negative correlations were found for SEGI

height, diameter at breast height (DBH), and diameter at half tree height at age 14 with elevation of native grove origin (Melchior and Herrmann 1987). Cold damage has also been related to elevation of native grove origin, with groves from higher elevations more resistant to freezing damage (Guinon et al. 1982). The FSO study site is located in the Sierra Nevada, north of all native SEGI groves but at a lower elevation than most SEGI groves. The SEGI propagules planted at FSO have origins in grove samples from high and low elevations from throughout the north-south latitudinal species range allowing for investigation of the relationship of these native grove geographic characteristics to SEGI growth outside of the native range.

1.3 Morphological Traits of SEGI and Timber Utilization

Observations in the native SEGI groves and in field plantings of SEGI have noted several form traits that are thought to have an underlying genetic basis. These traits may pose challenges to the efficient harvesting of SEGI and milling of SEGI logs leading to poor recovery of milled timber. Of particular interest are SEGI’s tendency to exhibit fluting, asymmetry, and basal swelling of the lower stem as well as epicormic sprout formation and low height-diameter ratio. The presence of these traits may lead to decrease in wood volume for milling (basal swelling, fluting, stem taper) or defects of the wood, such as knot formation (epicormic sprouting) or wood rot (fluting). These traits are likely strongly influenced by environmental factors, such as spacing among trees and crown position in the canopy. However, identifying the influence of genetic sources of variation in these traits is of ecological interest and of concern to land managers who may

want to plant SEGI for wood production. If specific native groves or regions of grove origin can be identified that express more favorable tendencies in these traits, then the losses in wood volume or growth efficiency associated with negative expressions of these traits may be avoided. There has been little published information addressing these traits in SEGI.

Fluting is a trait expressed in many forest trees in which slower diameter growth of certain areas of the stem results in a pinching or inward folding of the stem (Day 1964, Coutts and Philipson 1975, Fayle 1981). This phenomenon may be caused by differential stimulation of the cambium due to environmental factors such as crown position or may be a genetic trait of the species. Fluting reduces the amount of recoverable wood volume in a butt log since flutes may extend deep into the log, exaggerate taper, and can make logs hard to stack or handle (Harris and Farr 1974). In SEGI trials planted in Beaumont, New Zealand, fluting depth of SEGI was greater in trees with larger diameters at age 26 (De La Mare 2004). Trees with deeper flutes also had greater incidence of heart rot in the Beaumont trials necessitating the culling of up to one meter of the butt log prior to milling. If there is a strong relationship of SEGI native grove origin to severity or frequency of lower stem fluting, identifying this trend will help avoid selection of seed sources exhibiting this trait and the potential sawn timber recovery losses associated with the trait.

Basal swelling describes a distinct increase in the rate of taper in the lower portion of the stem (i.e. at or below DBH). It is thought to be a genetic trait of SEGI and has been observed on many SEGI planted in Europe (W.J. Libby, pers. comm.). Unlike young

SESE, which maintain fairly consistent tapering of the lower stem, many young SEGI demonstrate a swelling or flaring within the first one to two meters of the lower stem above the ground (Weatherspoon 1990). Basal swelling is considered a defect for wood production as the swelling comprises wood volume that may not be recovered at the sawmill. Observations of SEGI planted singly in parks have noted pronounced basal swelling of the lower bole (W.J. Libby, pers. comm.). Many of these planted SEGI, especially in Europe, originated from the North Calaveras grove, the site of the first scientific description of the species by European-Americans in 1853. This leads to the question of whether there is variation in this trait among the native groves or whether it is characteristic of the species. There are no known published data comparing the degree of basal swelling exhibited among SEGI propagules originating from a range-wide sample of the native groves. The common-garden trials at FSO allow for the investigation of among- and within- grove variation in this trait and will help fill this gap.

Epicormic sprouting in SEGI is common, though less common than in the closely related SESE (Weatherspoon 1990). Epicormic sprouting is assumed to be a response to a reduction in photosynthetic area or increased bole exposure to solar radiation or heat (Kozlowski and Pallardy 1997). It may be an adaptation to allow rapid replacement of lost foliage and regain photosynthetic area following damage to the crown or pruning of branches. In a study on early growth of SEGI propagules from the FSO seed collection, there was a trend of increased incidence of epicormic sprouting in SEGI originating from more southern native grove origins (Fins and Libby 1982). In SEGI trials planted at U.C.

Berkeley's Blodgett Forest Research Station, more severe pruning intensities led to an increase in epicormic sprout formation (O'Hara et al. 2008).

After 29 growing seasons at FSO, the SEGI propagules were of a size where these distinctive morphological characteristics were being expressed to a degree that assessment was possible. Identification of geographic or genetic variation in these traits for SEGI propagules planted at FSO will inform seed collection for timber production objectives. If among-grove variation in the morphological traits that are related to timber defect is prominent, certain native groves or regions may be avoided as seed sources. It will also help guide genetic conservation efforts by identifying specific native groves or regions of origin that exhibit distinctive morphological traits or unique attributes worthy of preservation or propagation.

1.4 Native SEGI Grove Structure, Inter-Specific Competition, and Climate Change

In recent times, the native SEGI groves have been restricted to montane elevations in the Sierra Nevada as part of the Sierra Nevada mixed conifer forest type (Tappeiner 1980). Common associates of SEGI are *Abies concolor* (ABCO), *Pinus lambertiana* (PILA), *Calocedrus decurrens* (CADE), *Pinus ponderosa* (PIPO), and, in the northern native groves, *Pseudotsuga mennziesii* (PSME). *Sequoiadendron giganteum* rarely forms pure stands within the native groves, typically occupying less than five percent canopy cover (Rundel 1971). In terms of density and canopy cover, in the recent past, the native SEGI groves were dominated by ABCO and PILA, while SEGI dominated in terms of basal area ($\geq$ 55%) (Rundel 1971). In drier or lower elevation sites,

CADE was more commonly found in the understory, while PIPO and PSME tended to be less common within groves and found on more xeric grove margins (Rundel 1972. Bonnicksen and Stone 1982). An example of a pure-SEGI stand composition occured in Redwood Mountain Grove where in an area less than 1 ha SEGI canopy cover was ~90% (Rundel 1971). Other examples of pure-SEGI stand composition have been noted in Converse Basin, Giant Forest, Garfield Grove, and Mountain Home (Rundel 1971, Willard 2000).

Soil water availability is thought to limit SEGI's extent within its current range SEGI's presence within the native groves (Ray 2016). Sites within grove boundaries with SEGI present had significantly greater soil water availability than sites on grove margins without SEGI present (Rundel 1972). In particular, winter snowmelt is an important source of soil moisture for SEGI through the dry growing season (Rundel 1972). The native range of SEGI is currently undergoing a period of rapid climate change in which conditions in the Sierra Nevada are predicted to become more xeric (Hayhoe et al. 2004, IPCC 2007), which may alter conditions within SEGI native groves to favor species found on drier sites such as PIPO and CADE over SEGI. Reductions of 37 - 79% in Sierra Nevada snowpack are predicted by the end of the century (Hayhoe et al. 2004).

Sequoiadendron giganteum typically outgrows other conifers in mixed species plantings throughout the Sierra Nevada and in Europe when soil moisture and site quality is high (Kitzmiller and Lunak 2012, Knigge 1993). In mixed species plantings at U.C. Berkeley's Blodgett Forest Research Station near Georgetown, CA, approximately 12 km south of FSO, PIPO had faster growth than SEGI at close spacing and higher stand

densities (Peracca and O'Hara 2008, York et al. 2013b). In particular, SEGI HT growth was more sensitive to crowding than usually observed for conifers. Both stem diameter growth and height growth of SEGI proceeded more slowly at higher densities (York et al. 2013b). Therefore, there is potential for co-occurring mixed conifer species to outcompete SEGI when planted in mixtures or within the native groves as climate change alters native grove habitat conditions.

1.5 Assisted Migration and Conservation Strategies

In order to prepare conservation strategies for SEGI native groves, a better understanding of SEGI response to drier and warmer conditions will be beneficial (Millar and Libby 1991). Common-garden trials, like those at FSO, planted outside SEGI's native range, offer an opportunity to increase this understanding. It is likely SEGI will not have time to adapt and migrate as it did during prior climate change events. Therefore, if seed collection and outplanting are required to preserve SEGI genetics, which groves should serve as seed sources for outplanting? Should seed be collected from trees or groves with distinctive morphological characteristics, or do these traits lack heritability? Where should outplanting be located, i.e. what geographic region? Should outplantings seek to encourage outcrossing by planting seed from different regions or native groves within these new groves?

1.6 Objectives

My thesis provides a fundamental base of knowledge on which to develop a comprehensive conservation strategy for SEGI. I have continued and expanded on the work on early performance of the SEGI propagules planted at FSO by Lauren Fins and William J. Libby (Fins 1979, Fins and Libby 1982). My study examined both population variation in a range-wide sample of SEGI propagules and the competitive effects between SEGI and five co-occurring mixed conifer species in three common-garden trials planted at the USDA Forest Service (USFS) Foresthill Seed Orchard (FSO) near Foresthill, CA in 1981.

I explored three overarching questions in my thesis: 1) Given these historic expansions and contractions of SEGI populations, how is genetic diversity of the species structured among and within these disjunct grove populations? 2) How do current native grove geographic characteristics, such as grove size, latitude, and elevation relate to growth of SEGI propagules outside of their current range; 3) How does competition from species of mixed conifers and brush that co-occur with SEGI in the native range affect SEGI growth outside of its native range. Additionally, I consider how scenarios for climate change in the Sierra Nevada range may affect the growth, competitive ability, distribution, and conservation of the species.

The primary objective of this thesis is to identify population variation in tree size and form traits of SEGI propagules from 23 grove samples in a range-wide common-garden study after 29 growing seasons. A further goal is to relate this population variation in grove samples to geographic characteristics of their native grove origin including latitude, grove isolation by distance among groves in the native range, elevation, and total

grove area. I assessed the genetic architecture of SEGI by partitioning variation in SEGI tree size and form traits into hierarchical genetic sources among-regions, among-groves and among-clones. I analyzed patterns in the genetic architecture of SEGI for trends related to the latitude, elevation, and grove area of native grove origins. The SEGI traits examined included tree size parameters, fluting and asymmetry of the lower stem, basal swelling, fullness of the live crown, and epicormic sprouting, and heartwood decay resistance in cut stumps.

I hypothesized that native grove geographic characteristics and grove isolation were strong influences on SEGI performance and morphology at FSO after 29 growing seasons. Specifically, based on earlier studies of the propagules planted at FSO, I expected grove samples originating from central and southern native groves to perform better than the grove samples from the disjunct northern groves with regards to tree size traits. Likewise, I expected grove samples from lower elevation native groves to perform relatively better than grove samples from higher elevation origins. Grove area was not investigated for significance in the studies of early SEGI growth at FSO, but anecdotal evidence suggested that grove samples originating from larger area native groves would perform better than grove samples from smaller native groves, particularly the tiny Placer and Deer Creek groves, which I expected to perform poorly.

There is less information available on SEGI morphological traits from earlier studies at FSO or other plantings upon which to base hypotheses. I expected epicormic sprouting to be more abundant and more frequent in grove samples from more southern grove origins. I expected fluting of lower stems would be positively related to tree size,

as was seen in SEGI trials in New Zealand (L.E. Freer, unpublished data), but would likely exhibit no difference among-regions or among-grove samples. I expected basal swelling to be more prominent in North Calaveras grove samples and for moderate differences to be expressed among all grove samples. I had no information to base hypotheses regarding lower stem asymmetry or crown fullness upon, so anticipated no differences among-regions or other geographic characteristics.

I expected variation in all tree size and form traits to be high and distributed largely within populations (among-clones) and somewhat less among-populations (among-groves). I expected genetic variances in tree size traits to differ based on region of native grove origin (north, central, and south). I expected form traits to have larger genetic variance components and higher heritabilities than tree size traits like height that are strongly related to fitness and survival. This follows Fisher's (1930) fundamental theorem of natural selection, which states that any trait directly related to an organism's fitness will display lower genetic variance and thus lower heritability (Falconer and Mackay 1996). I expected SEGI's mixed conifer associates that grow well in drier locations, such as PIPO and PILA, to exert greater influence on growth of neighboring SEGI in mixed species plantings. I expected ectomycorrhizal species of trees and shrubs to grow better together than endomycorrhizal species. I expected no difference in heartwood decay among cut stumps of different native grove origins. If among-grove variation was high at FSO, it may be possible to identify grove samples that were superior in tree size or form traits and direct seed collection to the best performing native

groves as seed sources for future SEGI plantings. Taken collectively, the findings reported in this thesis will help inform future SEGI conservation and management.

2. MATERIALS AND METHODS

2.1 Study Site

Three SEGI common-garden trials were established in spring 1981 at the Foresthill Seed Orchard (FSO) on the Tahoe National Forest and have been maintained by the USFS. The site is located 32 km (20 mi.) east of Auburn, CA at 39°05´N, 120°43´W on the western slope of the Sierra Nevada range at an elevation of approximately 1,250 m. The FSO study site is north of the northernmost limit of the current range of SEGI at Placer Grove (39°03´N, 120°34´W) (Fig. 1). The study site is 150 m lower in elevation than the lowest elevation native grove with propagules planted at FSO, North Calaveras grove, and approximately 550 m lower than the absolute mean elevation of all native SEGI groves sampled at FSO (Table 1). The soils at FSO are characterized as Andesitic mudflow of the Ahart series on a ridgetop with a gentle west-facing slope.

Summaries of climate data for the Foresthill Ranger Station, approximately eight km west of the plantation, indicated that mean annual precipitation at this nearby location was 1,300 mm (51.3 in) with a mean of 663 mm (26.1 in) falling as snow each winter for the period 1980 to 2009 (WRCC 2014, http://www.wrcc.dri.edu). Mean depth of snowpack was approximately 25 mm for the months January to March (WRCC 2014). In comparison to a subset of SEGI native groves sampled at FSO, the study site experiences greater mean growing season temperature and greater mean growing season precipitation

(Thornton 2013, Table 2) with the growing season defined as May to September. In this subset of native groves, annual precipitation, growing season precipitation, and growing season temperature all declined from north to south (Table 2). Annual precipitation at Foresthill, CA was approximately equal to the two northernmost groves in the table and was greater than the more southern groves by 200 – 400 mm (Table 2).

2.2 Seed Ccollection and Creation of Cloned Sets

To investigate the genetic architecture of SEGI, seeds were collected from each of 23 of the 75 named native SEGI groves currently recognized by Save-the-Redwoods League (http://www.savetheredwoods.org) in a range-wide seed collection the summer and fall of 1974-1976. The 23 grove sample collection sampled the north to south range of the species including all eight of the disjunct northern native groves (Table 1). In each native grove sampled, seed was collected from one squirrel-cut cone collected at distances of >100 m from the previous collected cone to ensure that each cone came from a different parent tree. One cone per sampled location was used to reduce unknown double-sampling of families from collecting cones that may share the same female or pollen parent. This method was used in all but the Placer Grove, where so few trees were present and producing seed that shooting cones from trees was the only way to ensure that each cone collected came from a different parent tree (Fins 1979). Each sampled cone in a grove location constituted an open-pollinated (o-p) family.

Propagules were vegetatively produced from each of a sample of germinated seedlings by rooted cutting, henceforth known as stecklings. Ideally, each seedling donor

tree, or ortet, provided four steckling ramets, together which constituted a clone. Two ramets of each clone were then randomly deployed in both trial 1 and trial 2. As of 2009, only two clones had two ramets surviving in both trial 1 and 2. However, the clones with at least two surviving ramets in one of the trials as of 2009 comprised a clone subset of data allowing the assessment of an among-clone component of genetic variation for assessed traits within each trial.

In establishing the FSO trials, equal numbers of two-ramet clones per o-p family, and of o-p families per grove was desired but not achieved. This was due to variation in numbers of families originally sampled from groves, varying germination histories of these families in the nursery, and differential survival of ramets per ortet during rooting and post-rooting in the greenhouse. In order to meet an acceptable minimum number of clones-per-family and families-per-grove, data from samples of the Cedar Flat and South Fork groves, which are adjacent to one another in the native range, were treated together as one “grove” sample (Mahalovich 1985). Black Mountain I and II grove samples originated from the same geographic native grove and were split into two grove samples due to a high number of available and surviving stecklings.

2.3 Experimental Design and Planting History

2.3.1 Trial 1 experimental design and planting history pure SEGI planting

Trial 1 at FSO was designed to investigate variation among SEGI populations in a pure-stand planting of SEGI and covers approximately 2 ha. At the time of planting, the SEGI population samples consisted of 299 clones from 144 open-pollinated (o-p)

families from 23 grove samples (i.e. populations) planted in 63 single- and 472 double-planted locations with 1007 total stecklings (i.e. rooted cuttings).

The planting design of FSO trial 1 was a hexagonal interlocking design made up of three internal sets (Libby and Cockerham 1980). Trees were planted at three meter triangular spacing with each tree surrounded by six neighbors at equal distances forming a hexagonal pattern. The SEGI steckling grove samples comprised Set A of the three interlocking internal sets and were planted in even-numbered rows. The stecklings had been raised to field-ready conditions at the University of California Russell Reserve in Lafayette, CA. The other two internal Sets B and C were systematically planted in odd-numbered rows. Half of Sets B and C were planted with USFS seedlings collected from six SEGI native groves, hereafter referred to as SEGI seedling grove samples: North Calaveras, Redwood Mountain, Giant Forest, Cedar Flat, Garfield, and Mountain Home. The SEGI seedling grove samples were raised at the USFS tree improvement center in Chico, CA. The other half of Sets B and C were planted with eight “standard” clones of SEGI from six native groves, hereafter referred to as SEGI standard clones: two each from Merced and Cedar Flat, and one from North Calaveras, Windy Gulch, Grant, and Mountain Home groves. These SEGI standard clones were random multiple-ramet clones produced vegetatively as stecklings from Lauren Fins’ 23-grove seed collection prior to the SEGI steckling population samples as rooting techniques were being refined, first at the Albany, CA McGill Tract and then at the U.C. Russell Research Station. Each SEGI steckling grove sample tree within the hexagonal planting pattern at FSO thus had as

nearest neighbors first six and later three random SEGI drawn from the six seedling grove samples and the eight standard clones for a pure SEGI planting.

Two border rows consisting of 278 locations were planted to minimize environmental edge effects. The border rows were composed of SEGI seedlings, standard clones, and population-sample stecklings and were not included in the reported analyses. Including seedlings, standard clones, and border rows, a total of 1890 locations were planted at an initial density of 945 stems per hectare.

At the time the FSO trials were planted, it was thought that a SEGI tree could be transplanted to replace a dead SEGI at another location within the experimental site and still be included in the eventual analysis. The mostly anecdotal information on early growth of SEGI at that time suggested that SEGI growth tended to “check” (i.e. produce negligible above-ground growth) for several years upon planting before beginning a period of rapid growth. This was not the case at FSO and led to many disqualified individual SEGI trees in both trials due to abnormally slow growth following transplanting. Most locations were double-planted with identical propagule type as insurance against expected mortality.Trees that were transplanted from a double-planted location to replace mortality at locations where both trees died were not included in summaries and analyses. This is an indication of the lack of data-based information available on SEGI germination and early growth prior to the seed collection, nursery experiments, and field trials established using propagules from the 23-grove seed collection planted at FSO. In the event that both propagules survived the first planting

season, the individual in the northern planting location was analyzed for growth characteristics and the southern individual was transplanted or culled.

2.3.2 Trial 2 experimental design and planting: mixed conifer planting

Trial 2 at FSO was designed to investigate growth of SEGI steckling population-samples in a mixed-conifer setting. As in trial 1, the planting design was a hexagonal interlocking design made up of three internal sets with trees planted at three meter spacing. Trial 2 covered a smaller area than trial 1 at approximately 1.5 ha. The internal Set A was made up of the SEGI steckling grove samples raised at the U.C. Russell Research Station. At the time of planting, the population-samples consisted of 229 clones from 84 families from 22 grove samples planted in 451 locations spread throughout the trial. The 22 steckling grove samples were the same grove samples planted in trial 1 with the exception of Deer Creek trees for which the minimum number of two clones from two families were not available.

Interplanted with Set A, Sets B and C were seedling samples of SEGI and five mixed-conifer species typical of native SEGI groves. The SEGI seedlings were from the Garfield grove sample. The mixed conifer seedlings included ABCO, CADE, PILA, *Pinus ponderosa* (PIPO), and *Pseudotsuga menziesii* (PSME). The mixed-conifer seedlings were of local provenance (Foresthill, zone 525.40) with the exception of the CADE seedlings which were from a provenance test (Harry 1984). Two border rows were planted with these mixed-conifer seedlings and with SEGI seedlings from the Redwood Mountain grove. As in trial 1, the border row trees were not included in the

statistical analyses that follow. The total number of planted locations in trial 2, including border rows, was 1650 for an initial planting density of 1100 stems per hectare.

2.3.4 Trial 3 SEGI, mixed conifer, and brush competition planting

Trial 3 at FSO was designed to investigate SEGI seedling growth in a mixed conifer setting with three brush competition treatments. Trial 3 was smaller than trial 1 and 2, covering approximately 0.3 ha. Trees were planted in alternating rows of pure SEGI and mixed conifers at close spacing (1.5 m x 3.0 m). The planted SEGI seedlings were from seedling grove samples from North Calaveras, Cedar Flat, and Garfield groves. The same five mixed conifer species planted in trial 2 from the same local seed sources, ABCO, CADE, PSME, PILA, and PIPO, were planted in trial 3.

The SEGI and mixed conifer seedlings were planted in six blocks with three brush treatments applied to two blocks each. Under the bare ground treatment, blocks were kept free of brush competition. The *Ceanothus* treatment involved sowing seed and planting two local *Ceanothus* species and the *Arctostaphylos* treatment involved sowing seed and planting two local *Arctostaphylos* species as follows: planting the conifers, locally collected seeds of the two *Ceanothus* species, *Ceanothus integerrimus* and *C. cordulatus*, and two *Arctostaphylos* species, *Arctostaphylos patula* and *A. viscida*, were broadcast in the appropriate blocks. In addition, local seedlings of these same brush species were transplanted from nearby sites into the experimental blocks.

In the years since planting, the bare ground plots were well-maintained by the USFS and kept clear of invading brush species. Likewise, the brush plots were maintained so that only the appropriate brush species have remained in their original

plots. In the *Ceanothus* plots, the *C. integerrimus* was more successful than the *C. cordulatus* so that most of what remained in the trial was *C. integerrimus* along with another local *Ceanothus* species that invaded and was allowed to remain, *Ceanothus prostratus*. In the *Arctostaphylos* plots, the *Arctostaphylos patula* was more successful and largely dominated the site (W.J. Libby, pers. comm.).

The original trial 3 planting in spring 1981 consisted of 683 trees of all conifer species for a planting density of 2200 stems per hectare. Rows of SEGI were partially thinned in 1991 and 1999. Due to watering with sprinklers in dry periods of 1981 and 1982, mortality was largely limited to ABCO and blister-rust infected PILA. As of 2009, trial 3 consisted of 156 mixed conifers, of which 71 were SEGI seedlings.

2.3.5 Nursery-effect and thinning of the trials

Thinning a decade after planting in 1991 reduced competition in the SEGI trials at FSO. Thinning removed primarily SEGI seedlings and standard clones in Sets B and C in trial 1. In trial 2, the thinning partially removed mixed conifer seedlings. In the early years of growth at FSO, SEGI steckling growth in both trials lagged behind that of the SEGI and mixed conifer seedlings. This lag in SEGI steckling growth was attributed to a nursery-effect experienced by the SEGI steckling grove samples raised at the coastal U.C. Russell Research Station. In order to prevent this nursery effect from confounding the FSO SEGI steckling data, the trials were divided to limit competition between the stecklings and the generally taller SEGI and mixed conifer seedlings.

A second thinning in 1999 divided both trials into two experiments within each trial respectively. One experiment in each trial was dedicated to a pure SEGI steckling

population-sample study for the analysis of growth, genetic architecture, and patterns of geographic variation in SEGI stecklings. In trial 1 this study occupied approximately 75% of the trial area, while the southern 25% became a pure SEGI seedling study with trees from six SEGI seedling grove samples to investigate among-grove differences in performance and morphology. The remaining “standard” clones in trial 1 were confined to border rows. After thinning in 1999 in trial 1, there remained 477 SEGI trees for a stand density of 239 stems per hectare. In trial 2, thinning in 1999 divided the trial so that the pure SEGI steckling grove sample study occupied approximately 50% of the eastern portion of the trial. The other 50% remained a mixed conifer planting with SEGI seedlings from the Garfield grove sample growing in mixture with the five mixed conifer seedlings to investigate competitive effects within this mixed species planting. After thinning in 1991, in trial 2 there were 463 trees remaining for a stand density of 308 stems per hectare.

In addition to differences arising from propagation in different nurseries, factors with potential to confound results from genetic experiments include differences in spacing unbalancing neighbor competition, uneven effects of competing vegetation, and disturbances or treatments that have unequal impact on the development of trees. With some exceptions, the thinning treatment preserved approximately even spacings among residual trees, except in trial 1, where a note was made of suspected competition with large trees outside of the fenced experiment. In the years since the last thinning, the FSO trials have been kept free of competing vegetation by the USFS. All surviving trees have

been pruned to approximately 2 m above the ground level or to half tree height if tree height was ≤ 4 m.

2.4 Data Collection

In summer 2009, measurements were made on all live trees in the three trials at FSO for height (HT09) in meters (m) and stem diameter at 1.37 m breast height (DBH09) in centimeters (cm). In trial 1, measurements were made on 477 SEGI trees of which 296 were steckling grove samples with 257 in interior locations and 39 border trees; 100 were seedling grove samples; and 81 were standard clones. In trial 2 measurements were made on 463 trees of which 283 were SEGI including 150 steckling grove samples in interior locations and 133 SEGI seedling-samples with 37 in interior locations. The other 180 trees were mixed-conifer seedlings of five species with 127 in interior locations.

In addition to 2009 data, individual tree height (HT) data were available from previous measurement years in 1981 (HT81), 1983 (HT83), 1988 (HT88), 1991 (HT91), and 1997 (HT97). Stem diameter (DBH) data were available from measurement years in 1991 (DBH91) and 1997 (DBH97). These past data allowed for comparison of tree size and growth of trees at FSO over 29 growing seasons.

Using this individual tree HT and DBH data, three additional variables were calculated in order to describe tree size and growth at FSO. These variables include conic stem-volume index (VOL) in cubic meters (m^3) and height to diameter ratio (HDR) for measurement years 1991, 1997, and 2009. Equations for these derived traits follow:

$$\mathrm{VOL}_i = \pi * (DBH_i/200)^2 * (HT_i/3) \quad (1)$$

$$\text{HDR}_i = (HT_i * 100)/DBH_i \quad (2)$$

In each equation the HT and DBH values are individual tree values for the *i*th tree.

To assess individual tree growth rate relative to individual tree size at FSO, I calculated mean relative growth rate (RGR) (Blackman 1919) for individual tree HT increment, DBH increment, and VOL increment for each periodic measurement increment for which data on these traits were available: HT increments from 1981 to 1983 (RGRh83), 1983 to 1988 (RGRh88), 1988 to 1991 (RGRh91), 1991 to 1997 (RGRh97), and 1997 to 2009 (RGRh09); DBH increments from 1991 to 1997 (RGRd97) and 1997 to 2009 (RGRd09); and VOL increments from 1991 to 1997 (RGRv97) and 1997 to 2009 (RGRv09). The equation for RGR is as follows:

$$\text{RGR}_i = (ln(S_{it_2}) - ln(S_{it_1}))/(t_2 - t_1) \quad (3)$$

In this equation, *ln* is the natural logarithm, S_{it_1} is tree size of the *i*th individual tree in the measurement year at the beginning of the measurement period (t_1) and S_{it_2} is tree size of *i*th tree in the year at the end of the measurement period (t_2). The denominator of this equation is the difference in years between the end of the measurement period (t_2) and the beginning of the measurement period (t_1). This produces RGR in measurement units per unit per year depending on the assessed trait. For HT, RGR was expressed as meters per meter per year (m m^{-1} yr^{-1}). This equation has been used to assess relative growth rate of conifers in common-garden experiments previously (Sweet and Wells 1974, Brand 1991). This RGR equation was assumed to eliminate differences in growth

rate that result from initial size differences (Wareing 1966). However, a tree with a smaller mean tree size but same periodic annual increment as another tree will have a larger relative growth rate (Burdon and Sweet 1976, South et al. 1988).

In addition, I assessed SEGI trees for five tree-form traits including fluting of the lower stem (FLUT), asymmetry of the lower stem (ASYM), basal swelling (SWEL), fullness of the live crown (FULL), and abundance of epicormic sprouts (EPI). Each trait was assessed on a four-point scale from 0 to 3 in which 0 was minimal expression of the trait and 3 was maximal expression of the trait as observed at FSO.

The lower stem-form characteristics were assessed on four-point scales while making allowances for size differences among the trees. Lower stem fluting (i.e., irregular grooves or furrows in the lower stem) was assessed based on a combination of the number and depth of flutes with “0” being no incidence of fluting and “3” being more than 4 flutes or extremely deep flutes relative to the size of the bole. The asymmetry trait was defined as departure from a circular or cylindrical cross-section in the lower-bole. A tree receiving a “0” had an approximately cylindrical stem, a “1” was slightly oblong, a “2” had at least one prominent buttress depending on severity, and a “3” was nearly flat on one side and round on the other like a half moon, or had other severe departures from a circular lower-bole cross-section. Basal swelling was assessed as the departure from taper in the lower portion of the stem with “0” being a continuation of taper (i.e., no swelling), “1” and “2” indicating either a relatively small or large increase in the rate of taper, and “3” being an abrupt swelling or major increase in the rate of stem taper

(resulting in stem diameter increases of ≥ 50% of the stem diameter from top to bottom of the swollen portion of the stem) within one meter of ground level.

For the assessment of crown fullness, the four point scale varied from “0”, a tree with sparse crown confined to extremities of branches, to “3”, a tree with a full and dense crown with little to no light passing through the combined branches to the observer. Epicormic sprouts were counted on the lower stem below the live crown and each tree was assigned a value from 0 to 3 depending on the number of sprouts. A tree receiving a “0” had no epicormic sprouts, a “1” had 1-3 epicormic sprouts, a “2” had 4-6 epicormic sprouts, and a “3” had >6 epicormic sprouts on the pruned portion of each stem to a height of two meters above ground level.

In 2010, I evaluated the heartwood decay resistance of stumps of SEGI seedlings and standard clones thinned in 1999 within trial 1. There were 188 SEGI seedling stumps from all six SEGI seedling grove samples and 119 stumps of standard clones from all eight standard clone grove samples thinned in 1999 and available for assessment. After 11 years growth before thinning in 1999, these thinned stumps were large enough that heartwood development had occurred and could be assessed for decay resistance. The eleven years since thinning at the time of assessment in 2010 allowed sufficient time for decay to occur and ye these had not disintegrated.

Heartwood decay resistance assessed on a four-point scale varying from “0” for heartwood that was mostly decayed, “1” for heartwood that had large amounts of decay with some resistance, “2” for heartwood with small amounts of decay that was mostly resistant, to “3” for heartwood that was structurally sound with minimal decay. Only

stumps that were in their original planting location based on the trial 1 map were evaluated. This meant that no loose stumps or stumps that had been uprooted were evaluated.

In summation, I collected data for analysis of eleven growth, form, and heartwood resistance characteristics at FSO in 2009 and 2010 including: HT, DBH, VOL, HDR, RGR, FULL, EPI, FLUT, ASYM, SWEL, and heartwood decay resistance of thinned stumps. Each trait was calculated on an individual tree basis with summarized means for grove sample, region, grove size category, planting stock type, and trial based on unweighted means of individual tree values.

2.5 Analyses

At the time of data collection in 2009, there were 257 SEGI stecklings from 23 grove samples in trial 1 and 150 SEGI stecklings from 22 grove samples in trial 2 planted in interior locations within the trials. Data for trees that had confounding events in their nursery or plantation history were removed from the sample along with any trees with visible defects such as broken tops. A group of five stecklings on the east side of trial 1 closest to Foresthill Divide Road were very small and likely had depressed height growth from competition with large oaks planted along the road. Data for these five trees were removed from the sample. After removal of these disqualified trees, the total number of SEGI steckling population-samples consisted of 237 SEGI stecklings from 23 grove samples in trial 1 and 124 SEGI stecklings from 22 grove samples in trial 2. Summaries of descriptive statistics by grove sample for trial 1 and trial 2 were produced with this individual tree SEGI steckling data.

Due to past findings regarding the unusual growth of Placer and Deer Creek grove samples (Fins and Libby 1982), all data for these trees were excluded from the majority of statistical analyses. This resulted in 21 grove samples per trial consisting of individual tree growth and form data for 227 and 119 SEGI stecklings in trial 1 and trial 2 respectively for a total of 346 SEGI stecklings across the two trials. This dataset was used for analysis of SEGI steckling grove sample variation.

To investigate the relationship between SEGI steckling growth and geographic characteristics of grove sample origin in the native range, the 21 grove samples from

trials 1 and 2 were grouped according to the region and grove-size of native grove origin (Table 1). The 21 grove samples per trial divided into three even groups of seven grove samples per analyzed “region” – north, central, or south – of grove sample origin in the native range. The 21 grove samples were divided into four groups based on the area of the native grove of origin, from small to very large. The Placer and Deer Creek grove samples were grouped together in a tiny grove size category to demonstrate their difference from the other grove samples, but were not included in statistical tests. These groups were used previously in the studies of early growth of the SEGI stecklings at FSO (Fins and Libby 1982, Mahalovich 1985).

The north region group comprised the seven disjunct northern native groves from North Calaveras (38.3° N) to McKinley (37.0° N). The central region group comprised the seven sampled native groves from Cabin Creek (36.8° N) to Giant Forest (36.6° N). The south region group comprised the seven sampled native groves from Atwell Mill (36.5° N) to Packsaddle (35.9° N). The five native grove-size categories – tiny (Placer and Deer Creek), small (≤ 100 ha), medium (~100-350 ha), large (~350-1000 ha), and very large (>1000 ha) – resulted in three grove samples in the very large category, six each in the large, medium, and small categories, and two groves in the tiny category.

Descriptive statistics of measured tree size traits for SEGI grove sample stecklings were summarized by regional groups and native grove size groups in trial 1 and trial 2 independently. Differences among the regions and grove-size groups were tested for significance in one way ANOVAs. If statistically significant differences were detected among groups, I used a Tukey-Kramer multiple comparison test to identify

significant pairwise differences between groups. Residual plots were examined to assess assumptions of normality of residuals and homogeneity of variances. I used the Shapiro-Wilk's test for normal distribution of residuals and the Fligner-Killeen test for homogeneity of variances among groups (Conover et al. 1981). If either of these failed, I used the Kruskal-Wallis test, which is the non-parametric equivalent of one way ANOVA.

In several tables and figures, descriptive statistics and significance tests depict differences among trials, grove samples, regional categories, grove size categories, or propagule types as a percent of the grand mean. In these tables and figures, the standard error bars were relative standard errors (RSE) calculated by dividing the standard error of the group mean by the group mean and multiplying by 100 to express RSE as a percent of the group mean.

The non-parametric Spearman rank-order correlations (r_s) were used to determine phenotypic correlations among all measured traits and native-grove geographic characteristics for latitude, grove area, and elevation. The Spearman rank-order correlations do not require data to meet assumptions of normality. Correlations were done independently for SEGI steckling and seedling individual tree data.

2.5.1 Variance-components analyses of hierarchical levels of genetic organization

To investigate rangewide SEGI genetic architecture, a subset of trial 1 and trial 2 SEGI steckling data were analyzed to partition variation in measured traits into genetic sources of variation. These subsets consisted of all surviving and eligible two-ramet clones from SEGI steckling grove sample data. Each two-ramet clone consisted of two

genetically identical steckling trees produced from rooted cuttings from the same ortet. In trial 1 there were 50 available two-ramet clones for a total of 100 stecklings. In trial 2 there were 17 of these two-ramet clones available for a total of 34 individual stecklings. These two subsets will be referred to as clone subsets in the description of the analysis that follows.

There were not adequate numbers of clones with two surviving ramets in both trial 1 and trial 2 for an analysis of among-clone variance across the two trials at FSO. Nor were there sufficient number of grove samples in both trial 1 and trial 2 with at least two clones with two surviving ramets to analyze clone-within-grove sample variance across the two trials. For this reason, the analysis of hierarchical levels of genetic variation across the two trials required the creation of a subset of data comprised of only single ramet stecklings. One ramet from all two-ramet clones was selected randomly for inclusion in the subset in addition to all surviving single-ramet stecklings. Two grove samples, Merced and Grant, lacked the requisite minimum of three single-ramet stecklings so no data were included in this analysis from those grove samples. This reduced the total number of grove samples from 21 to 19 for this analysis. This also resulted in an unequal number of grove samples within each region leaving six grove samples within the north and central regions and seven grove samples within the south region. This subset of the data included 19 grove samples per trial with 161 stecklings in trial 1 and 98 stecklings in trial 2 for a total of 259 single-ramet stecklings across the two trials and hereafter will be referred to as single-ramet subset data.

Using the clone subsets and single ramet grove sample subset, variance components were calculated from ANOVAs of each measured trait with hierarchical sources of genetic variation as factors. The variance components were obtained by dividing the mean square error of each hierarchical source of genetic variation by the harmonic mean number of samples within each level of variation. The percent contribution of each variance component to the total variation in each trait was calculated and summarized in tables for all measured tree size and form traits in three independent analyses of hierarchical levels of genetic variation: trial 1 among-clone variance, trial 2 among-clone variance, and across-trial variance components. For each analysis, broad-sense heritabilities were calculated estimating the ratio of total genetic variation to total phenotypic variation in each trait. Data from five past measurements from 1981 to 1997 were available to assess trends in genetic sources of variation and heritabilities over time at FSO. Details of each analysis follow below.

The subset of clones from trial 1 and trial 2 were used to obtain variance components within each trial independently for hierarchical sources of genetic variation among-regions and among-clones in each measured trait at FSO over 29 growing seasons. This analysis included factor variables in an ANOVA for region and clone sources of variation. To obtain the variance component for each source, the mean square error for each factor level was subtracted from the mean square error of the next factor level and divided by the harmonic mean number of samples within that level. The harmonic mean number of clones within regions in trial 1 was 16.5 and in trial 2 was 5.4. The harmonic mean number of ramets within clone was two. The among-region (σ_r^2)

variance in this analysis was an estimate of the portion of total phenotypic variance among-clones in each trait attributable to variation among geographic regions within each trial. The among-clone (σ_c^2) variance was an estimate of the portion of phenotypic variance attributable to variation among-clones. The sum of the among-region and among-clone variances in this analysis was an estimate of total genetic variance (σ_g^2) for each measured trait at FSO. The inclusion of the two ramets at random planting locations in each trial allowed for the interpretation of the within-clone or error variance (σ_e^2) of the model as an estimate of the environmental variance in each trait. Given that the two ramets of each clone were genetically identical, variation among-ramets within-clones was largely attributable to environmental variance within the trial. From these variance components, an estimate of broad-sense heritability, the ratio of genetic variance to total phenotypic variance of a trait, was calculated for each measured trait in trial 1 and trial 2 independently with the following formula:

$$H^2 = \frac{\sigma_g^2}{\sigma_g^2 + \sigma_e^2} \qquad (4)$$

where H^2 is the broad-sense heritability, σ_g^2 is the total genetic variance, σ_e^2 is the error variance, and their sum is the total phenotypic variance.

The single-ramet subset data allowed for the estimation of range-wide hierarchical levels of genetic variation across the two trials at FSO. In this analysis, there was no among-clone variance component since only one ramet of clones with both surviving ramets was included in the data. This analysis included factorial variables for each hierarchical level of population variation: trial (σ_t^2), region within trial (σ_r^2), grove within

region (σ_g^2), the interaction of trial and grove (σ_{txg}^2), and residual error (σ_e^2). The residual error term in this analysis included within-grove, environmental, and error variance. Harmonic means of the number of regions within trials was three, groves within region was 6.3, and ramets within groves varied from 6.9 in trial 1 to 4.3 in trial 2. From the variance components an estimate of range-wide broad-sense heritability was calculated with the following equation:

$$H^2 = \frac{\sigma_g^2}{\sigma_t^2 + \sigma_r^2 + \sigma_g^2 + \sigma_{txg}^2 + \sigma_e^2} \quad (5)$$

where H^2 is broad-sense heritability, grove-within-region variance (σ_g^2) is the estimate of total genetic variation, and the sum of all variance components in the model above is total phenotypic variance.

2.5.2 Effect of geographic characteristics of SEGI grove sample origin on SEGI height after 29 growing seasons

I used linear mixed effects regression models to analyze the effect of geographic characteristics of SEGI grove sample origin in the native range on the response variable SEGI HT09 for trial 1 and 2 SEGI steckling data from 21 grove samples (n = 346). The Fligner-Killeen (Conover et al. 1981) test indicated a lack of homogeneity of variance between HT09 data in the two trials ($p \leq 0.05$). To achieve homogeneity of variance, the trial 1 and 2 data were standardized by within-trial standard deviations. The standardization of the trial data produced equal standard deviations of one in trial 1 and 2 steckling data respectively, giving homogeneity of variance between the two trials ($p = 0.9$).

Past studies examining the interaction of latitude and elevation along the Pacific Coast of North America have noted that isotherms increase southward at 137 meters per degree latitude (Mote 2006). That is, relative to a site that is further north, a site with lower latitude has an effective elevation that is 137 meters lower than its actual elevation. To account for this, a latitude-adjusted elevation (Mote 2006) was calculated for each sampled native grove that referenced latitude to the Placer Grove, the furthest north of the sampled native groves. Latitude-adjusted elevation of a given grove was defined as

$$E_{\text{adjusted}} = E - 137(L_{\text{Placer}} - L) \quad (6)$$

with E as the true median elevation in meters of a grove sample, L_{Placer} is the latitude of the northernmost Placer Grove, L is the latitude of the given grove sample, and E_{adjusted} is the latitude-adjusted elevation (AdjEl) in meters.

My objective was determining the set of geographic characteristics that were the best predictors of SEGI HT09 at FSO after 29 growing seasons. The full mixed effects model consisted of fixed effects for latitude of native grove origin (Lat), grove isolation in terms of mean distance to the two nearest groves in the sample in decimal degrees of latitude (DIST), the latitude-adjusted elevation of native grove origin (AdjEl), and area of native grove in hectares (GA). A random effect for grove sample (n = 21) was included in the model. This random effect accounted for the lack of independence among observations of the individual steckling geographic characteristics within grove samples, a source of pseudo-replication in the data.

I analyzed models with response variable SEGI HT09 and covariates of the full model of grove sample geographic characteristics following a stepwise regression

procedure. I first extracted variance inflation factors (VIF) using *corvif* function in R statistical software and eliminated any covariates with VIF >3 (Zuur et al. 2010). I selected the best model from the remaining candidate set of models using Akaike's information criterion (AIC). The lowest scoring model by AIC was deemed "best" (Burnham and Anderson 2002). I considered all models within three AIC points of this best model as statistically viable models (Burnham and Anderson 2002). I assessed the likelihood of each model being the best model using Akaike's information criterion weights (AIC_w). The AIC_w is a likelihood transformation of raw AIC values. A model with an AIC_w of 0.60 is interpreted as having a 60% likelihood of being the best model compared to the other models and given the data (Burnham and Anderson, 2002).

Prior study of the SEGI trees planted at FSO led to the observation that several of the best-performing grove samples had a history of harvesting of SEGI and non-SEGI species within native groves (W.J. Libby pers. comm.). These harvesting events in the late 19th and early 20th centuries may have led to waves of SEGI regeneration that are better adapted to a warming 20th c. climate (W.J. Libby, pers. comm.). To test the effect of harvest history on the response SEGI HT09 at FSO, a categorical fixed effect for harvest (Harv) or no harvest (UnHarv) was included in the full model described above. The same model selection method was followed using AIC and AIC_w in model selection. However, most of the grove samples planted at FSO with a history of harvesting originated in native groves categorized as large or very large groves. To account for the correlation of grove area and harvest history, this analysis utilized a subset of stecklings from only the large or very large grove samples. This resulted in a large grove sample

subset with 68 trees in four UnHarv grove samples and 95 trees in five Harv grove samples. The full linear mixed effects model contained fixed effects for all geographic characteristics of grove sample origin, a categorical fixed effect for harvest history, and a random effect for grove sample (n = 9).

2.5.3 Comparison of SEGI seedlings and stecklings

The trial 1 SEGI seedling grove sample data consisted of 79 seedlings from six grove samples. I used one way ANOVAs to test for significant differences among the seedling-grove samples.

In addition, I analyzed the five SEGI seedling grove samples and corresponding steckling grove samples for significant differences between the two types of planting stock at FSO for all assessed traits. These analyses included SEGI seedlings and stecklings from North Calaveras, Redwood Mountain, Giant Forest, Cedar Flat/South Fork, and Mountain Home grove samples for a sample size of 68 seedlings and 63 stecklings. There were no stecklings planted from Garfield grove so I excluded the Garfield seedling grove samples from the analysis data. I used the non-parametric Kruskal-Wallis test for significant differences among planting stock because the steckling and seedling data did not meet the assumptions of normally distributed residuals and homogeneity of variance required for ANOVA.

2.5.4 Trial 2 SEGI seedling in a mixed species planting

In the mixed species half of trial 2 there were 32 SEGI seedlings and 112 mixed conifer seedlings of five species in the analysis data. The five mixed conifer species planted in trial 2 with SEGI were ABCO, CADE, PSME, PILA, and PIPO which all co-

occur with SEGI in the native range. Data were available for summary and analysis of height in 1983 and 1986 abd of all measured tree size traits for three measurement years in 1991, 1997, and 2009. There were no form trait assessments made on the five co-occurring mixed conifer species for comparison with SEGI seedling form data in trial 2.

I tested for significant differences among the species using one way ANOVAs for all measured size traits for each of 3 - 5 measurement years. If statistically significant differences were detected among species, I used the Tukey honest significant differences test (TukeyHSD) to perform multiple comparison tests between individual species within the group. Residual plots were examined to assess assumptions of normality and homogeneity of variances. I used the Shapiro-Wilk’s test for normal distribution of residuals and the Fligner-Killeen test for homogeneity of variances among species groups (Conover et al. 1981). If either of these failed, I used the Kruskal-Wallis test, which is the non-parametric equivalent of one way ANOVA.

I conducted a nearest neighbor analysis on the SEGI seedlings testing the competitive effects of the six mixed conifer species, including SEGI, on SEGI seedling periodic annual stem diameter growth increment from 1997 to 2009. I compared total neighborhood competition of SEGI subject trees as estimated by five distance-dependent competition indices (CI) (Table 3) as well as the sum of neighborhood cross-sectional basal area at breast height (BA) and the sum of neighborhood stand density index (SDI), both of which included the subject tree, as controls. For each CI, I calculated the competitive influence of the neighboring tree relative to the size of the SEGI subject tree and the distance of the neighboring tree from the subject tree in a given neighborhood

size of 4, 5, 6, 7, 8, 9, 10, and 11 m radius circle centered on the SEGI subject tree. The trees at FSO were planted in a hexagonal planting pattern with three meter spacing between nearest neighbors. Due to past thinning of the trial, CI neighborhood sizes with a circular radius less than four meters resulted in too many SEGI subject trees with zero near-neighbors for statistical analysis.

In calculating the CI's at varying neighborhood sizes, I included data for all individual trees in trial 2, including border trees and disqualified transplants, to account for all potential competitive effects on SEGI subject trees. One possibly confounding factor in this analysis was that thinning of trial 2 occurred in 1999, two years after the 12-year increment period analyzed here began. There were therefore competitive effects for some SEGI subject trees for the two year period prior to thinning in 1999 which were not accounted for in this analysis. I calculated CIs for all neighboring trees of each SEGI subject tree in R statistical software adapted from code originally written by Adrian Das. Total neighborhood CI was the sum of neighbor tree CI at a given neighborhood radius for each SEGI subject tree. I also summed neighbor tree CI by species to obtain an estimate of the total competitive effect of each species present in a given neighborhood size for each SEGI subject tree, hereafter referred to as species-specific CI.

I analyzed total neighborhood competition models and species-specific models of competition for all six conifer species present in trial 2 on SEGI subject tree DBH increment (DINC) from 1997 to 2009. I used a linear model of SEGI subject tree DINC as a function of total neighborhood CI at a given radius for each candidate CI to determine the best combination of CI and neighborhood size. I determined the best model

by Akaike's information criterion corrected for small samples (AIC_c) with the lowest scoring model deemed best (Sugiura 1978). I considered all models within three points of this best model statistically viable models (Burnham and Anderson 2002). I used Akaike's information criterion weights (AIC_w) to assess the likelihood that the chosen model was the best model of the candidate models analyzed.

Once the best CI was selected, I analyzed the individual competitive effects of the six mixed conifer species planted in trial 2 in a linear model of SEGI subject tree DINC as a function of species-specific CI. Each species-specific CI was a covariate in the full model. I used a stepwise procedure based on AIC_c scores, with lower scores better, to determine which set of species-specific CIs produced the best model of SEGI subject tree DINC. I also used AIC_w to assess the likelihood that the best model was the best model of all candidate models analyzed.

2.5.5 Trial 3 mixed species and brush competition

I used SAS® software version 9.2 (SAS Institute 2008) to test for differences in stem volumes of the six conifer species in a mixed effects model. The model included the main effects species, treatment, edge, and the interaction effects of species × treatment and species × edge. Block was treated as a random factor and all other variables were fixed. Least square means were estimated for species × treatment as well as effect slices for species and treatment. I ran a multiple comparison test to identify significant differences between treatment effects within each species.

2.5.6 Heartwood stump decay analysis

I used ANOVA to test for differences among SEGI seedling grove samples and among SEGI standard-clone stumps thinned in 1999 in independent analyses. The ANOVAs also tested the significance of region (north, central, south) of SEGI seedling sample and standard-clone sample native grove origin on heartwood decay resistance of the thinned stump samples.

The SEGI seedling stumps allowed for an assessment of the significance of variation among SEGI grove sample origins for heartwood decay resistance. The standard clone stumps allowed for an estimation of variation in heartwood decay resistance among and within the eight standard clones.

2.5.7 Statistical software

I conducted all statistical analyses with R statistical software (*R Development Core Team*) unless otherwise noted. I used package lme4 (Bates et al. 2015) in R statistical software to fit linear mixed effects models and obtain Akaike's information criterion (AIC_c) corrected for small sample sizes.

3. RESULTS

3.1 Performance and Morphology of SEGI Steckling Grove samples over 29 Growing Seasons at FSO

In this common-garden study of SEGI planted at FSO in spring 1981, steckling grove samples were planted in two trials, a pure SEGI planting (trial 1) and a mixed species planting with SEGI interplanted with five co-occurring mixed conifer species (trial 2). Mean size and form traits of stecklings differed between the two trials, but the same grove samples in each trial performed best. Means were reported for Placer and Deer Creek grove samples, but these trees were omitted from all statistical tests.

3.1.1 Trial 1 SEGI steckling tree size traits after 29 growing seasons

There were statistically significant differences in mean HT09 among steckling grove samples in trial 1 ($p \leq 0.03$; df = 20; n = 227) after 29 growing seasons at FSO (Figure 2). Mean steckling grove sample HT09 in trial 1 varied from a low of 6.2 m for Placer (s.d. = 2.1 m) and Deer Creek (s.d. = 3.4 m) grove samples to a high of 12.0 m (s.d. = 3.1 m) for the Mountain Home grove sample. The overall grove sample mean in FSO trial 1 HT09 was 9.9 m (s.d. = 2.8 m) (Table 4).

Mean steckling diameter (DBH09) after 29 growing seasons was less variable than HT09 in trial 1 with a coefficient of variation (CV) of 24% compared to a CV of 29% for HT09 (Table 5 and 6). Mean steckling grove sample DBH09 varied from a low of 14.8 cm (s = 3.9 cm) in Placer grove samples to 33.8 cm (s.d. = 6.8 cm) in Mountain

Home grove samples. Mountain Home stecklings exceeded trial 1 steckling mean DBH09 by 28% (Table 6; Figure 3) and were 20% greater than the second ranked Converse Basin stecklings.

Mean conic stem volume varied more after 29 growing seasons (VOL09) than HT09 or DBH09 with a CV of 71%. Steckling grove sample means varied from a low of 0.04 m^3 (s.d. = 0.03 m^3) in Placer grove samples to 0.41 m^3 (s.d. = 0.27 m^3) in Mountain Home grove samples. The trial 1 steckling grove sample mean VOL09 was 0.21 m^3 (s.d. = 0.15 m^3). Mean VOL09 of Mountain Home steckling grove samples was 195% of the steckling mean. Giant Forest ranked second for mean VOL09 at 133% of the mean, but only third in HT09 and fifth in DBH09. The Converse Basin grove samples ranked third in VOL09 at 129% of the mean (Table 6; Figure 4).

Mountain Home steckling grove sample ranked first in the three assessed size traits. The difference between first ranked Mountain Home and second ranked Converse Basin grove samples was greatest in DBH09 and VOL09. This suggested that growing space availability and neighborhood competition effects varied as a result uneven growth and thinning in trial 1. The tallest and largest individual steckling in trial 1 was from the Mountain Home grove sample with VOL09 of 1.03 m^3, nearly 500% greater than the mean. This tree was on the edge of a sizable gap with nearest neighbor a North Calaveras steckling with VOL09 only one percent of the steckling mean. Two other large stecklings were nearby on the edge of this gap, another Mountain Home steckling and a Black Mountain 1 steckling.

Most steckling grove samples contained individual trees well below the steckling mean VOL09 (Table 4). The CV for this trait was largest of the size traits at 71% (Table 6). Notably, the minimum volume of an individual steckling in both the Mountain Home and Converse Basin grove samples was 0.14 m^3, which exceeded or equaled mean VOL09 of the four grove samples with the smallest means: Placer, Merced, Cedar Flat/South Fork, and Deer Creek. The smallest individual tree from the third ranking Giant Forest grove sample was 0.04 m^3, which equaled the mean of the lowest ranked Placer grove sample (Table 4).

The poorest performing steckling grove samples for tree-size traits were from the Placer and Deer Creek grove samples. These groves are geographically at the north and south SEGI range limits respectively. These grove samples ranked 22nd or 23rd for all three tree size traits, with mean VOL09 of Placer grove samples at 19% and Deer Creek at 38% of the overall mean (Table 6; Figure 4).

3.1.2 Trial 1 SEGI steckling growth over 29 growing seasons from 1981 to 2009

There were notable rank changes in SEGI steckling grove sample rankings for HT over 29 growing seasons at FSO. These rank changes occurred primarily in early growth of the trial prior to the first thinning in 1991. Following the thinning in 1991, ranks of grove sample mean HT in trial 1 were generally stable (Table 5). Differences in HT among grove samples were not significant in any measurement year until HT09 ($p \leq 0.05$).

After one growing season, Lockwood, Atwell Mill, and Windy Gulch ranked highest in HT81. The Atwell Mill and Windy Gulch grove samples had the highest native

grove elevations of all grove samples (Table 1), however elevation was weakly correlated with HT81 ($r_s = 0.06$) and with HT09 ($r_s = 0.06$). The grove samples that were tallest in HT09, Mountain Home and Converse Basin, ranked 20th and eighth in HT81 respectively. First season height at FSO was moderately correlated with year-29 height ($r_s = 0.24$; $p \leq 0.001$).

After three growing seasons at FSO, HT83 was strongly correlated with HT09 ($r_s = 0.61$; $p \leq 0.0001$). All three top-ranking HT09 grove samples ranked in the top third in HT83 and were above the steckling mean (Figure 6). Wheel Meadow grove sample ranked first in HT83 and ranked in the top half of the grove samples through the 29th growing season. After 11 growing seasons, the top three grove samples in HT91 (Figure 7) were the same as in HT09 (Figure 2) and the two measurement years were strongly correlated ($r_s = 0.79$; $p \leq 0.0001$). Following thinning the HT ranks were more stable (Table 5).

In the first measurement year DBH data were recorded, McKinley grove sample ranked first in DBH91 at 124% of the steckling mean ahead of Mountain Home and Converse Basin grove samples (Table 6). Black Mountain II ranked fourth in DBH91 at 113% of the steckling mean. Both McKinley, a north region grove sample, and Black Mountain II, a south region grove sample, lagged in DBH97 to 105% and 95% of the steckling mean respectively. In DBH09, McKinley and Black Mountain II ranked 13th and 15th respectively. McKinley ranked third in mean VOL91 at 131% of the steckling mean behind Mountain Home and Converse Basin. McKinley VOL97 decreased to 101% of the respective means for an eighth place ranking. In VOL09, McKinley trees were

95% of the steckling mean for a 12th place ranking. Mountain Home grove samples ranked first in mean VOL91, 97, and 09 (Table 6).

An example of rank changes in grove samples from close geographic proximity, demonstrated the variability in steckling growth in trial 1 at FSO over 29 growing seasons. The North Calaveras and South Calaveras grove samples ranked eighth and ninth place in VOL91 at 112% and 110% of the steckling mean respectively. The North Calaveras and South Calaveras native groves are separated by less than 5 miles in the north region of SEGI's native range in the Sierra Nevada. North Calaveras grove samples fell to 92% of the mean in VOL97 and then to 65% of the mean and a 19th place ranking in VOL09. South Calaveras grove samples moved up the rankings to sixth place in both VOL97 at 117% and VOL09 at 114% of the respective trial 1 steckling means (Table 6).

Black Mountain I and II grove samples provided another demonstration of the variability in SEGI growth in trial 1 at FSO. These two grove samples share the same native grove within SEGI's native range. The stecklings comprising these two grove samples were produced from seed collected in the same native SEGI grove. The stecklings were arbitrarily assigned to two grove samples due to abundant survival. These two grove samples exchanged rank positions between VOL91 and VOL09. Black Mountain I grove samples ranked 13th at 92% of mean VOL91, while Black Mountain II ranked sixth at 116% of mean VOL91 (Table 3). In VOL09, Black Mountain I ranked seventh at 110% of steckling mean and Black Mountain II grove samples were 90% of VOL09 steckling mean ranking 14th (Table 6).

Mean relative height growth rate from 1981 to 1983 (RGRh83) differed significantly among steckling grove samples ($p \leq 0.01$) (Figure 8). The grove samples with fastest RGRh83 were Mountain Home (119%), McKinley (116%), South Calaveras (111%), and Wheel Meadow (109%). Mean relative height growth rate in this early period was more strongly correlated with HT09 and VOL09 than RGRh in any of the other time periods assessed ($r_s = 0.39$; $p \leq 0.0001$). Stecklings that had the most rapid relative height growth rate from the first to third growing seasons at FSO tended to be larger in 2009. The measurement interval from 1981 to 1983 was the wettest interval at FSO, with mean annual precipitation of ~1900 mm yr^{-1} (WRCC 2014). Mountain Home grove samples were the largest stecklings by VOL09 in trial 1, while South Calaveras grove samples were the largest stecklings of the north region grove samples.

I detected significant differences in RGRh91 among SEGI steckling grove samples in RGRh91 ($p \leq 0.05$) were statistically significant (Figure 9). During this period (1988-1991), canopy closure was occurring at FSO and the northernmost grove samples from Mariposa to Placer had above average RGRh91. Mariposa ranked first of all grove samples in this period with RGRh91 at 118% of the mean in trial 1. During this period of growth FSO experienced below average precipitation with 900 mm falling relative to the long term average of 1300 mm (WRCC 2014). Mean RGRh91 among stecklings in trial 1 from 1988 to 1991 was weakly correlated with HT09 ($r_{s=}$ -0.01) and VOL09 (r_s = -0.04).

The grove samples with fastest RGRh09 in the most recent period of growth measurement from 1997 to 2009, were Windy Gulch, Cabin Creek, Black Mountain II, Packsaddle, and Mariposa (Figure 10). Differences in growth rate for this period were not

statistically significant. Windy Gulch steckling grove samples were among the tallest individuals in HT83 (Figure 6), but severely lagged in the following years with the slowest RGRh91 at 78% of the mean (Figure 9). For the most recent period, Windy Gulch had the fastest RGRh09 at 112% of the mean and these grove samples had above average VOL09 at 104% of the mean, up from a low of 90% of mean VOL91. Mariposa was the only north region grove sample with RGRh09 above the trial mean for this period. The four southernmost grove samples in the trial all had above average RGRh09 (Figure 10). Mean annual precipitation at FSO during the period 1997 to 2009 was approximately average at 1350 mm yr^{-1} (WRCC 2014).

3.1.3 Trial 1 SEGI steckling height-diameter ratio from 1991 to 2009

After 29 growing seasons, mean height-diameter ratio (HDR09) of SEGI stecklings in trial 1 was 37.4 (s.d. = 5.3) (Table 4). The grove sample with the largest mean HDR09 was Black Mountain II (μ = 42.2; s.d. = 3.5) and the lowest was Merced (μ = 31.1; s.d. = 3.4) (Table 4). Trial 1 HDR09 was less variable than HT09, DBH09, or VOL09 with a CV of 14%. Trial 1 HDR09 was moderately positively correlated with VOL09 ($r_s = 0.33$; $p \leq 0.001$). An example of this weak correlation between HDR09 and VOL09 was provided by the contrasting HDR09 in trial 1 for the largest grove samples by mean VOL09. The Mountain Home grove sample with largest mean VOL09 had mean HDR09 six percent below the mean ranking 16th. Giant Forest and Converse Basin, ranking second and third in VOL09, had mean HDR09 5% and 9% greater than the mean ranking fifth and third in HDR09 respectively (Figure 11). The two smallest grove samples by VOL09 also demonstrated contrasting different rankings for HDR09.

Stecklings from the Placer grove sample had one of the highest mean HDR09 of 42 while Deer Creek stecklings had one of the lowest HDR09 of 33 with nearly equal mean HT09 for the two grove samples (Table 4).

Height-diameter ratio decreased with age at FSO. Mean HDR91 was 43.6 (s.d. = 14.9) with a CV of 34%. Mean HDR97 mean was 36.5 with a CV of 19%. In non-parametric statistical tests of trial 1 SEGI stecklings (df = 20; n = 227), differences among grove samples were statistically significant for HDR97 ($p \leq 0.05$) and HDR09 ($p \leq 0.001$).

Mean HDR91 of Mountain Home and Converse Basin trees ranked in the bottom quarter of trial 1 at 87% and 91% of the mean respectively, while Giant Forest HDR91 was approximately equal to the mean. The correlation of HDR91 with VOL91 ($r_s = -0.86$; $p \leq 0.001$) and VOL09 ($r_s = -0.48$; $p \leq 0.001$) were strongly negative indicating larger stecklings were stockier.

3.1.4 Trial 1 SEGI steckling form traits after 29 growing seasons

In trial 1 at FSO, there were statistically significant differences among SEGI steckling grove samples in mean basal swelling (SWEL) of the lower stem ($p \leq 0.01$). Grove samples with the highest levels of SWEL in trial 1 were Cedar Flat/South Fork ($\mu = 140\%$; CV = 25%), Merced ($\mu = 138\%$; CV = 41%), and North Calaveras ($\mu = 123\%$; CV = 38%) (Figure 12). There were moderate levels of variation for this trait among grove sample means (CV = 39%). Of the grove samples with the largest mean VOL09 in trial 1, Giant Forest ($\mu = 120\%$; CV = 22%) and Mountain Home ($\mu = 120\%$; CV = 32%) had above average SWEL, while Converse Basin ($\mu = 90\%$; CV = 35%) expressed lower

levels of SWEL. Black Mountain I (μ =92%; CV = 43%) mean SWEL was below the trial mean, while mean SWEL in Black Mountain II (μ =105%; CV = 40%) was greater than the mean (Figure 12). These grove samples were propagated from seed collected in the same native grove.

There was moderate statistical significance among SEGI steckling grove samples in the assessment of asymmetry (ASYM) of the lower stem (p = 0.06) (Figure 13). Cedar Flat exhibited the highest levels of ASYM in trial 1 at 164% of the steckling mean with no variation among individual stecklings. Each of the three stecklings in this grove sample exhibited the maximum lower stem asymmetry observed in trial 1. Most grove samples had an individual scoring the maximum value and the minimum value for this trait. Packsaddle (134%; CV = 33%), Converse Basin (125%; CV = 32%), and Redwood Mountain (124%; CV = 44%) grove samples expressed higher levels of ASYM. Placer (61%; CV = 88%), Windy Gulch (66%; CV = 91%), and Atwell Mill (76%; CV = 60%) grove samples exhibited the lowest levels of this trait. Asymmetry of the lower stem had a strong positive correlation with fluting ($r_s = 0.62$; $p \leq 0.001$) and a moderate positive correlation with DBH09 ($r_s = 0.25$; $p \leq 0.01$) and VOL09 ($r_s = 0.23$; $p \leq 0.05$) in trial 1.

Lower stem fluting (FLUT) of SEGI stecklings in trial 1 was highly variable within and among grove sample means (Figure 14). The CV among grove samples was 114% for this trait and most grove samples had individual stecklings with high and low levels of FLUT. The two smallest grove samples by mean VOL09, Placer and Deer Creek, exhibited no FLUT. The grove samples exhibiting greater amounts of FLUT included two of the top ranked groves by VOL09, Giant Forest (141%; CV = 104%) and

Converse Basin (138%; CV = 68%). The Converse Basin grove samples had the lowest amount of variation in FLUT among all grove samples exhibiting this trait. Fluting of the lower stem in SEGI stecklings was moderately and positively correlated to HT09 (r_s = 0.36; $p \leq 0.01$), DBH09 (r_s = 0.41; $p \leq 0.01$), and VOL09 (r_s = 0.41; $p \leq 0.01$) in trial 1.

Variation among-grove samples in fullness of the live crown (FULL) was moderate in trial 1 with CV = 54%. Grove samples from Grant (139%; CV = 22%), Mountain Home (125%; CV = 40%), and North Calaveras (123%; CV = 39%) ranked highest for FULL in trial 1 (Figure 15). Stecklings in Deer Creek (29%; CV = 100%) grove sample from the native grove at the southern range limit had the lowest FULL in trial 1, while the Placer grove samples (99%; CV = 119%), from the native grove at the northern limit, expressed average FULL. Both grove samples had the greatest variation in this trait in trial 1 by CV.

The mean level of epicormic sprouting (EPI) among SEGI steckling grove samples in trial 1 was the most variable trait assessed at FSO with a CV of 207% (Figure 16). Differences in mean epicormic sprouting among steckling grove samples was statistically significant at alpha = 0.1. Five grove samples exhibited no incidence of epicormic sprouting in trial 1 including three out of eight of the north region grove samples: Placer, Merced, and Nelder. The grove samples with the greatest mean level of epicormic sprouting were Cedar Flat/South Fork (437%; CV = 115%), Deer Creek (328%; CV = 141%), and Packsaddle (268%; CV = 143%), from the south region. Epicormic sprouting among SEGI stecklings in trial 1 was weakly negatively correlated to DBH (r_s = -0.23) and VOL (r_s = -0.22) indicating that smaller trees tended to produce

more epicormic sprouts. Demonstrating the great variability in this trait within grove samples, the Black Mountain I grove samples had no incidence of EPI, while Black Mountain II grove samples had above average mean EPI (164%; CV = 214%). The stecklings in these grove samples originated from the same SEGI grove within the native range.

3.1.5 Trial 2 SEGI steckling tree size traits after 29 growing seasons

After 29 growing seasons at FSO, in the block of trial 2 where SEGI stecklings were originally planted with mixed conifer neighbors subsequently thinned in 1999, mean SEGI steckling height (HT09) was 11.5 m (s.d. = 3.4 m) (Table 7; Figure 17). The grove sample with the tallest mean steckling HT09 was Mountain Home at 14.3 m (s = 3.9 m) and the shortest were from the Placer grove sample at 6.3 m (s.d. = 1.9 m). The maximum individual steckling HT09 in trial 2 was in the Converse Basin grove sample at 19.9 m. The minimum steckling HT09 was 4.2 m in the Placer grove sample (Table 7).

Mean diameter (DBH09) and volume (VOL09) of SEGI stecklings in trial 2 was 26.1 cm (s.d. = 6.9 cm) and 0.24 m^3 (s.d. = 0.20 m^3) respectively (Table 7). Mountain Home grove samples had the largest mean DBH09 (35.5 cm; s.d. = 5.9 cm) and VOL09 (0.51 m^3; s.d. = 0.31 m^3). Mean VOL09 of the top ranked Mountain Home grove sample was 209% of the trial 2 steckling mean (Figure 18). The minimum steckling VOL09 of the Mountain Home grove sample was 0.23 m^3, nearly equal to the trial 2 steckling mean. Converse Basin grove sample ranked second by mean VOL09 (0.44 m^3; s.d. = 0.44 m^3) at 180% of the mean with a large CV of 100% due to the influence of the largest individual SEGI steckling in trial 2 at 1.58 m^3. This tree was 60% larger than the next largest SEGI

steckling in trial 2, a Mountain Home steckling of 0.95 m^3. The minimum individual steckling VOL09 in Converse Basin grove sample was 0.06 m3, just 26% of the trial 2 steckling mean. The third ranked grove sample by mean VOL09 was Cabin Creek (0.35 m^3; s.d. = 0.26 m^3) at 144% of the trial 2 steckling mean. The Cabin Creek native grove is in close proximity in SEGI's native range to the Converse Basin native grove.

The Placer grove samples were the smallest stecklings in trial 2 at only 16% of mean tree volume (0.04 m^3; s.d. = 0.03 m^3) (Table 7). The next poorest performing grove samples by mean VOL09 were Tuolumne grove samples at 58% of the mean. Both North and South Calaveras grove samples had mean VOL09 below the mean, with South Calaveras performing better of the two at 90% of the trial 2 steckling mean. The most southern grove sample planted in trial 2 was Packsaddle which had mean VOL09 of 80% of the steckling mean. In trial 2 the differences among SEGI steckling grove samples in tree size traits were not statistically significant after 29 growing seasons.

<u>3.1.6 Trial 2 SEGI steckling growth over time 1981 - 2009</u>

The best performing SEGI steckling grove samples in terms of tree size in trial 2 were generally consistent throughout the six measurement periods from 1981 to 2009. As in trial 1, the largest and tallest steckling grove samples after 29 growing seasons were not among the tallest grove samples after one (HT81) and three (HT83) growing seasons at FSO (Table 8). Neither Mountain Home nor Converse Basin grove samples were top ranked in HT83, but both had mean HT83 greater than the steckling mean at 101% and 105% respectively (Figure 19). The correlation of HT83 with later HT09 was weaker in trial 2 ($r_s = 0.49$; $p \leq 0.001$) than in trial 1.

After 11 growing seasons, Mountain Home was top ranked at 126% of mean HT91 and Converse Basin was third at 116% of mean HT91. Giant Forest grove samples, which ranked fourth by VOL09, were second ranked at 119% of steckling mean HT91 (Table 8; Figure 20). Cabin Creek grove sample, third ranked by VOL09, had fast early height growth ranking first in HT83 at 143% of the steckling mean (Figure 19). After 11 growing seasons, Cabin Creek mean HT91 was 114% of the mean ranking fourth among steckling grove samples in trial 2 (Figure 20). During this same measurement period, Packsaddle grove sample fell from second ranked at 118% of mean HT83 to 12th in HT91 approximately equal to the mean (Figure 19 and 20). Correlation between HT91 after 11 growing seasons and HT09 after 29 growing seasons was strong in trial 2 ($r_s = 0.82$; $p \leq 0.0001$) and comparable with the same correlation in trial 1.

Other notable rank changes occurred in mean conic stem volume from 1991 to 1997, following thinning of trial 2 in 1991. Two north region grove samples went from above mean in VOL91 to below mean VOL09. Mariposa grove sample stecklings ranked fifth in VOL91 at 143% of the mean falling to seventh at 120% of mean VOL97 and 11th at 96% of mean VOL09. McKinley grove samples dropped from a VOL91 ranking of ninth at 107% of the mean to a ranking of 13th at 87% of mean VOL09. Lockwood, a central region grove sample had the greatest increase in VOL from 1991 to 2009 in trial 2. Lockwood grove samples were 64% of mean VOL91 ranking 19th rising to 85% of mean VOL97 and 102% of mean VOL09 for an eighth place ranking. Wheel Meadow dropped more gradually from 11th ranked in 1991 at 100% of the mean to a 15th place

2009 ranking at 83% of mean VOL (Table 9). Differences among steckling grove sample HT, DBH, or VOL were not significant in any of the measurement years.

Mean relative growth rate for height differed among grove samples in the period 1988 to 1991 (RGRh91) ($p \leq 0.05$) as crown closure was occurring (Figure 21). During this period the major rank changes in HT described above occurred (Table 8). Mean relative height growth rate from 1991 to 1997 (RGRh97) had a moderate to strong positive correlation ($r_s = 0.45$; $p \leq 0.001$) with VOL09, but differences in RGRh97 among grove samples were not significant (Figure 22). During this time stecklings in dominant crown classes took advantage of available growing space following thinning in 1991 to maintain these dominant positions in the canopy.

<u>3.1.7 Trial 2 SEGI steckling height-diameter ratios from 1991 to 2009</u>

Mean height-diameter ratio (HDR09) of SEGI steckling grove samples in trial 2 after 29 growing seasons at FSO varied from a low of 37.0 (s.d. = 1.4) for Merced grove samples to a high of 48.8 (s.d. = 5.7) for Windy Gulch grove samples (Table 7). The mean for all SEGI stecklings in trial 2 was 44.0 (s.d. = 7.2). In non-parametric tests, differences among grove samples in HDR09 ($p = 0.09$) were significant at alpha = 0.1 (Figure 23).

As in trial 1, HDR in trial 2 tended to decrease with advancing age. In trial 2, HDR was highest during crown closure after 11 growing seasons in 1991 at 46.5 (s.d. = 11.0) and lowest in 1997 at 40.9 (s.d. = 6.3) following thinning in 1991. As in trial, the correlation between HDR and VOL changed with age. Correlations of HDR91 with corresponding VOL91 ($r_s = -0.56$; $p \leq 0.0001$) and later VOL09 ($r_s = -0.53$; $p \leq 0.0001$)

were both strongly negative. Stecklings that were stockier at crown closure tended to have greater stem volume at age 11 and continued to produce more volume in subsequent growing seasons. After 29 growing seasons, the relationship between HDR09 and VOL09 was weakly positive ($r_s = 0.27$; $p \leq 0.001$) meaning more slender stecklings generally had larger stem volume in trial 2. This makes HDR an unreliable indicator of volume production as allocation of resources to height and stem diameter growth varies with age and stand density.

The two largest trial 2 grove samples by mean VOL09 demonstrated this contrasting relationship between HDR and VOL at FSO. Mountain Home grove samples, with the largest mean VOL09 in trial 2, had mean HDR91 ($\mu = 39.0$; s.d. = 3.3) and HDR09 ($\mu = 39.7$; s.d. = 4.4) below the trial 2 steckling mean by 16% and 10% respectively. Converse Basin grove samples ranked second in VOL09 and had higher mean HDR91 ($\mu = 46.8$; s.d. = 7.7) and HDR09 ($\mu = 45.6$; s.d. = 6.5) than Mountain Home, which were approximately equal to the trial 2 steckling mean. These results may be an indication that stecklings within grove samples differ in their resource allocation strategies. The same trends in HDR in these two grove samples were also observed in trial 1.

3.1.8 Trial 2 SEGI steckling form traits after 29 growing seasons

As of 2009, SEGI steckling grove samples with the greatest levels of basal swelling of the lower stem (SWEL) compared to the trial 2 steckling mean were North Calaveras (118%; CV = 29%), Tuolumne (117%; CV = 22%), and Mountain Home (118%; CV = 43%) (Figure 24). Packsaddle grove samples, originating at SEGI's

southern range limit, had the least amount of SWEL in trial 2 at 32% of the steckling mean with a high CV of 88%. However, differences among grove samples were not statistically significant in trial 2. Black Mountain 1 (108%; CV = 39%) grove samples had above average levels of SWEL, differing substantially from Black Mountain 2 (81%; CV = 60%) in this trait (Figure 24). The trend in these grove samples was reversed in trial 1, with Black Mountain I expressing low levels of SWEL and Black Mountain II expressing SWEL above the trial mean. These grove samples were propagated from seed collected in the same native grove.

Merced, Windy Gulch, Giant Forest, and Mountain Home grove samples expressed the greatest amounts of asymmetry (ASYM) of the lower stem in trial 2 (Figure 25). Packsaddle, South Calaveras, and Placer grove samples expressed the least ASYM. Differences among grove samples were not statistically significant for this trait. In trial 2, ASYM was strongly correlated to FLUT ($r_s = 0.64$; $p \leq 0.0001$) and moderately correlated to DBH09 ($r_s = 0.34$; $p \leq 0.001$) and VOL09 ($r_s = 0.35$; $p \leq 0.001$) indicating larger trees tended to have more asymmetrical lower stems.

In trial 2, fluting of the lower stem (FLUT) had high amounts of variation within and among grove samples. The coefficient of variation among all grove samples was 113% with a high of 224% for Placer and Cedar Flat/South Fork and a low of 70% for Nelder grove samples. The grove samples exhibiting the greatest mean FLUT in trial 2 include several of the top performers by mean VOL09 including Giant Forest (188%; CV = 115%), Converse Basin, and Cabin Creek (Figure 26). Nelder grove samples, which were 65% of mean VOL09, ranked second in trial 2 in mean FLUT at 169% of the mean

(CV = 70%). Fluting of the lower stem had moderate positive correlation with HT09 (r_s = 0.39; P ≤ 0.01), DBH09 (r_s = 0.40; P ≤ 0.01) and VOL09 (r_s = 0.42; P ≤ 0.01) indicating that taller, larger trees tended to produce more fluted lower stems in trial 2.

Crown fullness (FULL) of SEGI stecklings differed significantly (p ≤ 0.05) among grove samples in trial 2. The grove samples with the highest ranks for FULL in trial 2 were South Calaveras (218%; CV = 65%), Merced (174%; CV = 79%), and Placer (140%; CV = 66%) (Figure 27). Each of these were north region grove samples and in trial 2 there was a weak to moderate correlation of FULL with latitude of native grove (r_s = 0.20; p ≤ 0.05). In trial 2 FULL was more strongly and negatively correlated with native grove elevation (r_s = -0.26; p ≤ 0.01) indicating stecklings in grove samples propagated from higher elevation native groves tended to have sparser crowns at FSO. The grove samples with the lowest levels of FULL were Black Mountain 1, Packsaddle, and Atwell Mill. Atwell Mill grove samples were the highest elevation of the native groves planted at FSO. Black Mountain I and Black Mountain II grove samples, propagated from seed collected from the same native grove, differed in mean FULL with Black Mountain I at 54% (CV = 78%) of the trial steckling mean and Black Mountain II slightly above the mean at 102% (CV = 40%) (Figure 27).

Epicormic sprouting (EPI) was the most variable trait assessed in trial 2 with a coefficient of variation among grove samples of 259%. Ten of the 21 SEGI steckling grove samples exhibited no epicormic sprouting including most of the north region grove samples (Figure 28). Packsaddle, the southernmost grove sample in trial 2, produced the largest mean EPI at nearly 600% of the trial 2 steckling mean. Placer grove samples

(138%; CV = 224%) exhibited above average epicormic sprouting in trial 2. Differences in mean level of epicormic sprouting among SEGI steckling grove samples was statistically significant at alpha = 0.1 in trial 2.

3.1.9 Comparison of SEGI steckling performance and morphology in trial 1 pure SEGI planting and trial 2 mixed conifer planting

After 29 growing seasons at FSO, SEGI steckling mean height (HT09) was significantly greater in trial 2 (μ = 11.7 m; s.d. = 3.3 m) than trial 1 (μ = 10.1 m; s.d. = 2.7 m) ($p \leq 0.0001$) (Figure 29). Assuming that height growth of trees were free from competition – following thinning of both trials in 1991 and 1999 – was an indicator of site quality, the trial 2 site (upper slope) was a significantly better site for SEGI than the adjacent trial 1 site (ridge top).

Prior to thinning, the stecklings in trial 1 (μ = 2.5 m; s.d. = 0.7 m) were significantly taller than the trial 2 stecklings (μ = 2.2 m; s.d. = 0.5 m) in HT88 ($p \leq 0.0001$) (Figure 29). This was prior to crown closure when trees were relatively free to grow. At around the time of canopy closure in 1991 prior to thinning, trial 2 stecklings (μ = 4.4 m; s.d. = 0.9 m) were significantly taller than trial 1 stecklings (μ = 4.0 m; s.d. = 1.0 m). The stecklings in trial 2 were growing better with mixed conifer neighbors than the stecklings in trial 1 with SEGI steckling and SEGI seedling neighbors. At this time, stecklings in trial 2 were being outgrown in terms of HT91 by PIPO (μ = 6.4 m; s.d. = 1.1 m), PILA (μ = 4.6 m; s.d. = 1.2 m), and CADE (μ = 4.4 m; s.d. = 1.3 m) neighbors; in trial 1, stecklings were being outgrown by SEGI seedlings (μ = 4.8 m; s.d. = 0.9 m). Following thinning in 1991 and again in 1999, which removed mixed conifer neighbors

in trial 2 and SEGI seedling neighbors in trial 1, trial 2 stecklings continued to outgrow trial 1 stecklings with significant differences in both HT97 and HT09 (Figure 29).

Differences in mean relative height growth rates (RGRh) among trial 1 and 2 stecklings were statistically significant for each measurement period except for 1991 to 1997, the period following the first thinning of the trials (Figure 30). Trial 2 stecklings had the fastest RGRh from 1981 to 1983 ($p \leq 0.01$), while this result was reversed from 1983 to 1988 ($p \leq 0.0001$). In the period leading up to the first thinning from 1988 to 1991, trial 2 had faster RGRh. ($p \leq 0.0001$). In the most recent growth period, from 1997 to 2009, after removal of mixed conifer neighbors in trial 2 and SEGI seedling neighbors in trial 1, trial 2 had a significantly greater RGRh than trial 1 ($p \leq 0.001$) (Figure 30).

After 29 growing seasons, mean stem diameter at breast height (DBH09) did not differ between trial and trial 2 at FSO. There were no differences between the two trials in DBH91 or DBH97 either (Figure 31). Trial 2 steckling mean conic stem volume (VOL09) was greater in trial 2 than trial 1 after 29 growing seasons, but the difference was not significant (Figure 32). Nor were differences between the trials in VOL91 or VOL97 significant. With significantly greater height growth in trial 2 in HT91, HT97, and HT09, trial 2 mean height-diameter ratio (HDR) was significantly greater than trial 1 in each of the measurement years (Figure 33).

The best and worst performing grove samples within trial 1 and 2 were consistent after 29 growing seasons. In both trials Mountain Home, Converse Basin, and Giant Forest grove samples ranked highly for HT09, DBH09, and VOL09. The most notable difference in grove sample performance between the two trials was the relatively

better performance in trial 2 of several central region grove samples, particularly Cabin Creek. Cabin Creek grove sample ranked third in trial 2 in VOL09 44% above the within-trial steckling mean, while in trial 1 ranked 16th with mean VOL09 14% below the within-trial steckling mean.

In Kruskal-Wallis non-parametric ANOVAs, mean expression of form traits between trial 1 and 2 SEGI stecklings differed significantly for SWEL, FULL, and EPI at FSO after 29 growing seasons (Figure 34). Mean SWEL was greater in trial 2 than trial 1 stecklings ($p \leq 0.001$) (Figure 34). The only grove sample to express high levels of SWEL in both trials was North Calaveras. The crowns of stecklings in trial 1 had greater mean FULL by a highly significant margin ($p \leq 0.0001$). Mean EPI in trial 1 stecklings was significantly greater than in trial 2 stecklings ($p \leq 0.05$) (Figure 34).

3.2 Genetic Variation in SEGI Steckling Clones and Grove Samples over 29 growing Seasons at FSO

3.2.1 Variance components and genetic variation in trial 1 and 2 SEGI clone subsets

Genetic sources of variation in rangewide clonal subsets were generally moderate to high for SEGI size and form traits at FSO after 29 growing seasons.

Clonal variance in SEGI tree size traits

After 29 growing seasons at FSO, genetic sources of variation accounted for an approximately equal amount of phenotypic variation in SEGI HT09 at ~47% in trial 1 and 2 clonal subsets (Table 10). This was the largest genetic variance estimate in HT for all of the measurement years over the 29 growing seasons. The amount of phenotypic

variance in SEGI HT attributed to genetic sources was generally increasing in both trials over the 29 growing seasons (Figure 35), however, there were notable decreases in genetic variance in each trial at different periods of growth. In trial 1, genetic variance in HT88 decreased form HT83 levels. This was prior to crown closure and likely a free period of growth with clones growing more uniformly at this time. Genetic variance in HT in trial 1 increased in HT91 as crown closure approached and competition between neighboring trees likely became more of a factor within the trial. Genetic variance in HT97 and HT09 continued to increase following thinning of the trials in 1991 and 1999. In trial 2, genetic variance in HT97 declined following the thinning of the trials in 1991. Genetic variance in trial 2 HT09 increased to approximately the same level as in HT91 following thinning in 1999 (Table 10).

In several measurement years, the genetic variance estimates demonstrated large differences between the two trials. After three growing seasons, the genetic variance estimate in HT83 accounted for 36% of phenotypic variation in trial 2 and only 10% in trial 1. This large difference was greater in HT88 when genetic sources of variation accounted for 44% of phenotypic variation in trial 2 and only 7% in trial 1 (Table 10). As the crowns were closing in both trials after 11 growing seasons in 1991, differences between genetic variance in the two trials remained large, but decreased with an increase in genetic variance in trial 1 to 23%. These large differences in genetic variance were likely due to differing levels of stand density and competition in the pure SEGI planting of trial 1 and the mixed species planting of trial 2. Following thinning of the trials in 1991, genetic variance estimates in the two trials in HT97 were similar as trial 1 genetic

variance increased to 33% and trial 2 variance decreased to 38%. A second thinning occurred in 1999 in which the large SEGI seedlings were removed from competition with trial 1 SEGI clones and mixed conifer neighbors were removed from competition with trial 2 SEGI clones. At the next measurement following this thinning, genetic variances were equal in the two trials accounting for 47% of phenotypic variance (Table 10; Figure 35).

The amount of genetic variance in SEGI height over the 29 growing seasons at FSO differed between the two trials when partitioned into among-region and among-clone variances (Table 10; Figure 35). In trial 1, after one growing season on site, genetic sources of variation accounted for 11% of phenotypic variance. All of this was detected among-regions. The variance component among-clones was negative in trial 1 HT81. After three full growing seasons, all genetic variance was detected among-clones (18%) in trial 1 HT83, with a negative variance component estimate among-regions. The among-clone estimate decreased to 8% in HT88 as total genetic variance was at its lowest for HT in trial 1 in this year. Among-clone variance increased in HT91 to 23% as crown closure was occurring. Following thinning of the trial in 1991, among-clone variance continued to increase to its highest level in HT97 accounting for 33% of the phenotypic variance. Among-clone variance remained at this level in HT09 in trial 1. The among-region variance estimate was negative for HT88 to HT97 accounting for none of the phenotypic variance in HT in these measurement years. After 29 growing seasons, among-region variation accounted for a statistically significant 15% of phenotypic variance in HT09 and total genetic variance in trial 1 was highest in this year at 47%.

Among-clone variance was statistically significant in each measurement year from the 11th growing season (HT91) to the 29th (HT09) (Table 10).

In trial 2, there was no genetic variance detected in HT81 following the first full growing season. In HT83, among-clone variance accounted for 26% of phenotypic variance and among-region variance was 10% (Table 10; Figure 35). In trial 2 HT88, among-clone variance decreased to 13% while among-region variance increased to 31%. This trend continued in trial 2 HT91 with among-region variance increasing to 39% and among-clone variance decreasing to 7%, a level that was maintained in both subsequent measurement years following thinning of the trial in 1991 and 1999. Among-region variance decreased slightly in HT97 to 31% and increased in HT09 to 39%. Among-region variance was statistically significant in each measurement year from HT83 to HT09. Among-region variance accounted for a much greater proportion of phenotypic variance in trial 2 than it did in trial 1 and was statistically significant in each measurement year from HT88 to HT09. Among-clone variance was low in trial 2 from the third growing season onwards (Table 10; Figure 35).

In both trial 1 and trial 2 at FSO, the amount of phenotypic variance in DBH and VOL that was attributable to genetic sources was comparable to, but less than in HT (Table 10). In DBH and VOL in both trials, genetic variance increased from the first measurement in 1991 as crowns were closing to 2009 after 29 growing seasons (Figure 36 and 37). As with HT, the trends in partitioning of genetic variance to among-region and among-clone sources in these traits varied between the two trials.

In trial 1 all genetic variance in DBH and VOL was detected among-clones in 1991 and 1997 with among-region estimates negative in these years (Table 10). In 2009, among-clone variance increased for both traits to 24% in DBH09 (Figure 36) and 27% in VOL09 (Figure 37) and was greater than among-region variance. In trial 1, among-region variance was positive and statistically significant in these traits in 2009, accounting for 11% of phenotypic variance in DBH09 and 15% in VOL09. The among-clone variance was statistically significant in trial 1 in DBH09 ($p \leq 0.05$), VOL97 ($p \leq 0.05$), and VOL09 ($p \leq 0.05$) (Table 10).

In trial 2, all of the genetic variance in DBH and VOL was detected among-regions for each measurement year from 1991 to 2009. Among-region variance accounted for 18% of phenotypic variance in DBH91 and this increased to 45% in DBH09 ($p \leq 0.05$) (Table 10; Figure 36). Among-region variance in VOL91 accounted for 28% of phenotypic variance and this increased to 43% ($p \leq 0.05$) in VOL09 (Table 10; Figure 37). Among-clone estimates were negative in each measurement year for these two traits in trial 2 accounting for no phenotypic variance in DBH or VOL. Genetic sources of variation accounted for a greater proportion of phenotypic variance in DBH and VOL in trial 2 than in trial 1 in each measurement year (Table 10; Figure 36 and 37).

After 29 growing seasons, genetic sources of variation accounted for more phenotypic variance in height-diameter ratio (HDR) of SEGI clones in trial 1 and trial 2 than in any other trait assessed at FSO (Table 10). In trial 1, genetic variance accounted for 80% of phenotypic variance in HDR09 and in trial 2 52% of phenotypic variance in HDR09 was attributable to genetic sources. The genetic variance in HDR increased in

each measurement year from 1991 to 2009 in both trial 1 and 2 (Figure 38). All of the genetic variance detected in HDR in each measurement year from 1991 to 2009 occurred among-clones in both trial 1 and 2 (Figure 38). The among-clone variance estimates were statistically significant in trial 1 HDR97 ($p \leq 0.01$), HDR09 ($p \leq 0.0001$) and in trial 2 HDR09 ($p \leq 0.05$). The estimates of among-region variance in HDR were negative in each measurement year in trial 1 and 2 accounting for no phenotypic variance in this trait.

Clonal variance in SEGI form traits

Genetic variances in SEGI form traits in trial 1 and 2 clone subsets were moderate to high and comparable to genetic variance in size traits after 29 growing seasons at FSO for all traits except FLUT (Table 10). The trends in partitioning of genetic variances into among-region and among-clone sources observed in trial 1 and 2 for size traits was also demonstrated in form traits. In trial 1, all genetic variance occurred among-clones for all form traits, while in trial 2 a greater amount of genetic variance occurred among-regions than among-clones. The largest genetic variances occurred in form traits FULL and SWEL in both trial 1 and 2 and in ASYM in trial 2.

Of the form traits, genetic variance was largest in FULL in both trial 1 and trial 2 (Table 10). In trial 1, genetic variance accounted for 47% of phenotypic variance, all of this statistically significant amount occurring among-clones ($p \leq 0.0001$). In trial 2, genetic variance accounted for 50% of variation in FULL with 31% of this occurring among-regions and 19% among-clones. The among-region variance component estimate was statistically significant ($p \leq 0.05$). The SEGI clones produced from seed collected in the north region had higher FULL values than central and south region clones.

In trial 1, genetic sources of variation accounted for 34% of phenotypic variance in SWEL, all of it among-clones which was statistically significant ($p \leq 0.01$) (Table 10). In trial 2, genetic sources accounted for 24% of phenotypic variance in SWEL, with 17% occurring among-regions and 7% attributed to among-clone variance (Table 10).

In trial 1, there was no genetic variance detected in stem form trait FLUT. Variance components estimates of both among-region and among-clone sources were negative for this trait. All phenotypic variance in FLUT in trial 1 occurred at the level of within-clone residual error variance. This suggested that the variation in FLUT was related to environmental variation and not genetic sources of variation. In trial 2, a small amount of variance was detected among-regions in FLUT. This was not a statistically significant difference. The central region clones, largest by HT09 and VOL09 in trial 2, expressed mean FLUT 37% above the trial 2 SEGI clone mean. At FSO, the FLUT trait was significantly positively correlated with both HT09 ($r_s = 0.35$; $p \leq 0.0001$) and VOL09 ($r_s = 0.41$; $p \leq 0.0001$).

The genetic variances in ASYM differed more between the two trials than for any other form trait at FSO. In trial 1, a small amount of genetic variance in ASYM was detected among-clones, while in trial 2, genetic variance accounted for 40% of the phenotypic variance in this trait. Most of the genetic variance in ASYM in trial 2 occurred among-regions at 37% ($p \leq 0.05$). This large among-region variance was driven by the larger ASYM values in central region clones which expressed mean ASYM 34% greater than the SEGI clone mean in trial 2. Correlations between ASYM and VOL09 ($r_s = 0.23$; $p \leq 0.0001$) at FSO were weaker than with FLUT and VOL09, but still

statistically significant. The high among-region variance component may be related to this positive correlation of ASYM with VOL09.

The genetic variance estimates in EPI in trial 1 and 2 were approximately equal at 20% in trial 1 and 16% in trial 2 (Table 10). In trial 1, all of this variation occurred among-clones, while in trial 2 the variation in EPI occurred among-regions. The trial 1 estimate was moderately significant ($p = 0.08$), while the trial 2 estimate was not. This suggested that genetic control in EPI was weak to moderate and that the variation seen in this trait may have been due to differences in crowding and competition among trees within the trials.

<u>Heritability of traits from clonal subsets in Trial 1 and 2.</u>

After 29 growing seasons, estimates of broad-sense heritability (H^2) in trial 1 and 2 at FSO were moderate to strong for most traits and largely in agreement between the two trials. Heritability estimates of HT09 in trial 1 and 2 wereidentical with broad-sense heritability (H^2) in this trait of 0.47. This was slightly greater than, but comparable to broad-sense heritability estimates of DBH09 and VOL09 in trial 1 and 2 at FSO. Broad-sense heritability estimates for DBH09 varied from 0.35 to 0.45 in trial 1 and 2 respectively. Broad-sense heritability estimates of VOL09 in the two trials were nearly identical at 0.42 in trial 1 and 0.43 in trial 2. The strongest broad-sense heritability estimates were for HDR at 0.80 in trial 1 and 0.52 in trial 2. The data indicated that basal swelling (trial 1 $H^2 = 0.34$; trial 2 $H^2 = 0.24$) and crown fullness (trial 1 $H^2 = 0.47$; trial 2 $H^2 = 0.50$) were moderately to strongly heritable traits at FSO (Table 10).

3.2.2 Variance components for trial, region, and grove in combined Trial 1 and 2 steckling grove sample subset

In trial 1 and trial 2 SEGI single-ramet grove sample subset data, estimates of genetic variance and heritability were weaker than in the single trial estimates derived from clone subsets described above. In this variance components analysis, the largest source of variation for most traits and measurement years was among-trial variance (Table 11). There were large and significant differences between the trials that accounted for much of the variation in HT, HDR, and form traits SWEL, FULL, and EPI.

After 29 growing seasons, the largest source of variation in HT09 was trial variance accounting for a statistically significant 70% ($p \leq 0.0001$) of the phenotypic variance in this trait. The SEGI grove samples were significantly taller in trial 2 than in trial 1. Regional differences in HT09 accounted for 10% of the phenotypic variance, which was statistically significant ($p \leq 0.01$) and indicated the importance of region of native grove origin for HT growth of SEGI grove samples at FSO. Among-grove variance accounted for only 3% of the phenotypic variance in HT09 and was not statistically significant. Variation in HT09 among-regions was greater than variation among-groves within-regions at FSO. This trend was consistent for HT in all measurement years at FSO, except HT83 when a non-significant 5% of variation occurred among-groves. Among-region variation was at least moderately significant in all measurement years except HT83 after three growing seasons. At this time mean HT83 of north region grove samples was lagging behind the central and south region grove samples but the difference was not yet significant.

Variance components estimates for DBH attributed a statistically significant amount of phenotypic variance to among-grove variance in DBH97 ($p \leq 0.1$) and DBH09 ($p \leq 0.01$) (Table 11). The among-grove variance component estimate increased with age at FSO and in DBH09, accounted for 28% of phenotypic variance. This significant among-grove variation in DBH09 was due largely to the influence of Mountain Home grove samples, with all statistically significant differences in multiple comparisons tests among grove samples involving this grove. Mean DBH09 of Mountain Home grove was significantly larger than North Calaveras ($p \leq 0.0001$), Lockwood ($p \leq 0.01$), Redwood Mountain ($p \leq 0.01$), Atwell Mill ($p \leq 0.01$), Black Mountain 1 ($p \leq 0.01$), and Black Mountain 2 ($p \leq 0.01$), and Wheel Meadow ($p \leq 0.01$). A statistically significant estimate of 4% ($p \leq 0.1$) of phenotypic variation occurred among-regions in DBH09 with north region grove samples having smaller mean DBH09 at FSO than central and south region grove samples. There was no statistically significant variation among-trials in any measurement year for DBH in the SEGI single-ramet grove sample subset data (Table 11).

The largest source of variation in SEGI VOL09 occurred among-groves at 18% ($p \leq 0.05$). As with DBH09, this was due primarily to the influence of the Mountain Home grove. The strength of the among-grove variance component in VOL increased in each measurement year from 2% in VOL91 and 13% in VOL97. There was statistically significant variation in VOL09 among-regions at 16% ($p \leq 0.05$), with the central and south regions having significantly greater mean VOL09 than the north region grove samples. The only measurement year in which among-trial variance occurred in VOL

was in 1991 at 17%, which was non-significant (Table 11). In this year, trial 2 had greater mean VOL91 than trial 1.

Variance components estimates for HDR attributed a majority of phenotypic variance to among-trial variance in HDR97 and HDR09 (Table 11). In these measurement years 89% and 94% of phenotypic variance was accounted for by trial differences, with larger HDR in trial 2. Among-grove ($p \leq 0.05$) and among-region ($p \leq 0.05$) variance were both significant sources of variation in HDR09 though each accounted for just one percent of phenotypic variance. In HDR91, trial variance accounted for a large and significant 48% ($p \leq 0.05$) of phenotypic variance. There was a small but statistically significant amount of variation in HDR09 accounted for by region and grove. The mean HDR of central region grove samples were statistically significantly larger than the north region grove samples in multiple comparisons test.

The largest source of variation in SWEL, FULL, and EPI was trial variance with 76%, 83%, and 53% of phenotypic variance in these respective traits attributed to trial variation (Table 11). Mean SWEL was significantly greater in trial 2 ($p \leq 0.001$), while mean FULL ($p \leq 0.0001$) and mean EPI ($p \leq 0.01$) were greater in trial 1. Among-grove variance accounted for statistically significant amounts of phenotypic variance for each trait though only 5%, 4%, and 7% respectively occurred at this level. The only form trait for which among-region variance was a significant source of variation was EPI ($p \leq 0.1$) with 6% of phenotypic variance attributed to this level. Epicormic sprouting was greater in grove samples with origins in the south region of SEGI's range.

The single site clonal heritabilities derived from trial 1 and trial 2 independently (Table 10) were stronger than the SEGI single-ramet grove sample heritabilities from the combined trial 1 and 2 data (Table 11). The strongest heritability in the combined analysis was for VOL09 at 0.34. The heritabilities for HT09, HDR09, and the form traits were much lower, largely due to the large variation between the two trials. The among-trial source of variation in this data accounted for 70% of the variation in HT09, 94% in HDR09, and was >31% for all form traits other than FLUT. There was no among-trial variance detected for FLUT, DBH09, or VOL09. The broad-sense heritabilities for tree size traits increased with advancing age at FSO in this combined trial 1 and 2 data (Table 11).

3.3 Influence of Geographic Characteristics of SEGI Steckling Grove Sample Origin in the Native Range on Tree Size and Form Traits in Trial 1 and 2

3.3.1 Tree size related to region of SEGI grove sample origin

In summaries of SEGI steckling tree size by region of grove sample origin in the native range, mean tree size in both trials was greater in the central and south regions than the north region (Table 12) after 29 growing seasons. In trial 1, mean HT09 of central stecklings was 10.5 m (s.d. = 2.7) ($p \leq 0.01$) and south stecklings 10.6 m (s.d. = 2.9 m) ($p \leq 0.01$) were significantly greater than north region mean HT09 of 9.2 m (s.d. = 2.5 m) (Table 12; Figure 39). Central and south region steckling mean HT09 did not differ significantly from each other in trial 1 (Figure 39). In trial 2, central region steckling mean HT09 of 13.1 m (s.d. = 3.2 m) was significantly greater ($p \leq 0.01$) than

the north region mean of 10.6 m (s.d. = 2.9 m) and the south region mean of 11.4 m (s.d. = 3.2 m) (Table 12; Figure 39). The south region steckling mean HT09 did not differ significantly from the north region mean in HT09 (Figure 39).

In trial 1 steckling mean DBH09, patterns of statistical significance among-regions were identical to those in HT09. The central ($p \leq 0.05$) and south ($p \leq 0.05$) region DBH09 were significantly greater than north region stecklings, but did not differ from each other. In trial 2 mean DBH09, the central region again differed significantly from the north region stecklings ($p \leq 0.05$). The south region mean DBH09 did not differ significantly from either north or central region means (Figure 40). Steckling mean VOL09 in trial 1 and 2 followed the same respective trends within the trials as in HT09 and DBH09 (Table 12; Figure 41). In HDR09, the regional patterns of variation followed the same trends as in the tree size traits, but were weaker and lacked statistical significance.

The relationship of the form traits in SEGI stecklings to grove sample region of origin was generally weaker and less consistent than that of the tree size traits. There was a clear trend in SEGI stecklings in trial 1 and trial 2 of increasing mean epicormic sprout abundance (EPI) from the north to south region as of 2009. In both trials, south region mean EPI exceeded the steckling mean by at least 35%, while the north region mean was greater than 28% below the mean in each trial. This regional trend in EPI was not statistically significant due to the large variability within regions associated with this trait (Figure 42).

3.3.2 Tree size related to elevation of SEGI grove sample origin

There was a weak relationship of elevation of grove sample origin to SEGI steckling tree size and form after 29 growing seasons. In linear regression models of SEGI steckling HT09 on isotherm-adjusted elevation of grove sample origin, adjusted-R^2 approached zero. As an example, Atwell Mill grove samples, with the highest elevation origins at FSO by raw (2138 m) and adjusted elevation (1780 m), were moderately below-average performers with mean VOL09 of 90% of trial 1 steckling mean and 101% of trial 2 steckling mean.

3.3.3 Tree size related to area (ha) and harvest history of SEGI grove sample origin

The SEGI steckling grove samples with the largest mean tree size in both trial 1 and 2 at FSO had origins within SEGI's native range of large total grove area (Table 13 and 14). Mountain Home (1620 ha – very large) and Converse Basin (1498 ha – very large) were the two largest native groves by area with steckling grove samples planted at FSO. Both ranked in the top three for all tree size traits (Table 4 and 7). The smallest stecklings by tree size at FSO were in grove samples with native grove origins occupying smaller grove areas, such as Merced (8 ha - small), Tuolumne (8 ha - small), North Calaveras (24 ha - small), and Cedar Flat/South Fork (97 ha - medium) which ranked poorly for all size traits. As demonstrated in the trial 2 summaries by grove area categories, the relationship between grove area and steckling grove sample performance was not strictly linear with small groves outperforming medium groves in HT09 and medium groves outperforming large groves in DBH09. For all tree size traits, the very large area groves outperformed the smaller grove area groups (Table 14).

Several of the SEGI steckling grove samples from large area native groves which were performing well at FSO as of 2009 had been partially harvested for SEGI and/or mixed conifers prior to the seed collection that established the FSO trials. Summarizing the SEGI steckling size traits by harvested (Harv) or un-harvested (UnHarv) grove sample origins, the harvested grove samples had larger mean HT09, Harv = 11.5 m (s.d. = 3.2 m) to UnHarv = 10.2 m (s.d. = 2.9 m), DBH09, Harv = 28.3 cm (s.d. = 6.8 m) to UnHarv = 26.1 cm (s.d. = 5.6 m), and VOL09, Harv = 0.28 m^3 (s.d. = 0.22 m^3) to UnHarv = 0.21 m^3 (s.d. = 0.13 m^3). These differences were significant in Kruskal-Wallis one way ANOVA for HT09 ($p \leq 0.001$), DBH09 ($p \leq 0.01$), and VOL09 ($p \leq 0.001$). Of the seven grove samples at FSO with histories of harvesting, five of these were categorized as large or very large. All three of the very large grove samples had histories of harvesting within the native groves. This included the top performing Mountain Home and Converse Basin grove samples. Therefore, the correlation of harvest history with superior HT09 performance of stecklings produced from seed collected in these harvested groves may have been confounded with the effect of larger grove area on growth. To adjust for this effect, a subset of stecklings in only large or very large grove samples were summarized by harvested or un-harvested grove sample origins for tree size traits. In these summaries, the harvested grove samples again had larger mean HT09, DBH09, and VOL09, but were not statistically significantly greater than un-harvested grove sample means.

3.3.4 Linear mixed effects models of geographic characteristics of SEGI grove sample origin on SEGI height

In linear mixed effects regression models of range-wide combined trial 1 and 2 steckling grove sample standardized data, geographical characteristics of SEGI grove sample origin in the native range were analyzed for their relationship with the response variable SEGI HT09. The best model of SEGI steckling HT09 by AIC included covariates for native grove area (GA) in hectares and the mean distance to the two nearest native groves sampled at FSO in decimal degrees latitude (Dist) (Table 15). The covariate for latitude was dropped from the model due to a variance inflation factor > 3 indicating unacceptable collinearity. Without latitude in the model, the three other covariates had VIF values < 2, which is an acceptable level of collinearity (Zuur et al. 2010). According to Akaike weights of the candidate set of models, the selected model (GA + DIST) had a 49% probability of being the best model of the candidate set of models. The best model predicted greater HT09 from native groves that were larger in area and nearer to neighboring native groves (Figure 43). The predicted HT09 difference between a small 40 ha grove and a large 1000 ha grove was approximately 0.3 standardized units. The predicted difference in HT09 between an isolated native grove and a native grove nearly continuous with its nearest neighbors was approximately 0.25 standardized units (Figure 43).

Most of the grove samples with a history of harvesting within the groves, were larger groves by area. To account for this possibly confounding effect of native grove-area, harvest history of native grove of origin was investigated for a relationship with

SEGI steckling HT09 in a subset of SEGI stecklings including only trees in large or very large grove samples. In this analysis, the same linear mixed effects models and stepwise procedure was used as above with a binary categorical variable for harvest history of grove sample (Harv or UnHarv). The best model in this analysis by AIC included the variables for harvest history and adjusted elevation (Table 16). This model predicted greater SEGI steckling HT09 from grove samples with a history of harvesting in the native groves and originating from lower elevation native groves. The predicted difference in SEGI HT09 in a steckling from a harvested grove and an un-harvested grove was 0.6 standardized units. The predicted difference in SEGI HT09 in a steckling originating from a native grove with the lowest adjusted elevation (1210 m) at FSO and one from the highest (1780 m) was approximately 1.3 standardized units (Figure 44).

3.4 Trial 1 SEGI Seedling Grove Sample Performance and Morphology

3.4.1 Trial 1 SEGI seedling grove sample tree size traits

There were six SEGI seedling grove samples planted at FSO originating from seed collected in North Calaveras, Redwood Mountain, Giant Forest, Cedar Flat, Garfield, and Mountain Home groves in SEGI's native range. The best performing seedling grove sample after 29 growing seasons by HT09, DBH09, and VOL09 was Redwood Mountain grove sample (Table 17). Mean HT09 of Redwood Mountain seedlings was 14.0 m (s.d. = 3.4 m), 107% of the overall mean and 0.2 m greater than the second-ranked Garfield seedlings. Mean VOL09 of Redwood Mountain seedlings was 0.50 m^3 (s.d. = 0.27 m^3), 127% of the seedling mean of 0.39 m^3 (s.d. = 0.21 m^3) (Table

18). This was 25% greater than the second ranked Garfield grove with mean VOL09 of 0.40 m^3 (s.d. = 0.22 m^3). Most notable was the poor performance in VOL09 of the Mountain Home seedling grove samples, ranking fifth out of six, at 0.37 m^3 (s.d. = 0.18 m^3) or 94% of the seedling mean. This contrasts with the performance of the stecklings in the Mountain Home grove sample which were the largest steckling grove sample by a wide margin at 195% of the steckling mean at FSO. Garfield seedlings had the highest mean HDR09 among the seedlings at 43 (s.d. = 9.1) which was 107% of the seedling mean of 40 (s.d. = 5.1). There was little variation among SEGI seedlings in mean HDR09 which had a CV of 12.6%.

There were several notable changes in rank of seedling grove sample performance over the 29 growing seasons at FSO. After 11 growing seasons, Cedar Flat seedlings ranked second in mean VOL91 at 121% of the mean behind Redwood Mountain seedlings at 132% of the seedling mean (Table 18). In 2009, Cedar Flat seedling mean VOL09 was 100% of the mean ranking fourth, 27% lower than VOL09 of Redwood Mountain seedlings. North Calaveras seedlings fell from 90% of mean VOL91 to 79% of mean VOL09, though dropped only one place. Mountain Home seedlings ranked last in mean VOL91 at 77% of the mean and were 94% of mean VOL09 climbing one rank to fifth. There were no statistically significant differences among seedling grove samples detected for the tree size traits or height-diameter ratios in any measurement year.

3.4.2 Trial 1 SEGI seedling grove sample form traits

North Calaveras seedlings exhibited the greatest mean SWEL among the SEGI seedling grove samples at FSO (Table 19). The North Calaveras mean was 128% (CV =

21%) of the overall seedling mean. Giant Forest and Redwood Mountain seedling grove samples ranked second at 105% of the mean with CV = 39% and CV = 32% respectively. Garfield seedlings exhibited the least mean SWEL at 74% (CV = 37%). The differences in SWEL among seedling grove samples were statistically significant ($p \leq 0.01$).

Giant Forest expressed the greatest amounts of FLUT and ASYM of the lower stem among seedling grove samples (Table 19). These two traits were highly correlated among seedlings at FSO at $r_s = 0.59$ ($p \leq 0.01$). Giant Forest mean FLUT was 140% of the overall mean (CV = 83%) with 36% more FLUT than the Cedar Flat and Redwood Mountain seedlings. Giant Forest seedling mean ASYM was only 3% greater than second-ranked Cedar Flat seedlings and 19% greater than Garfield seedlings which exhibited the least ASYM among seedling grove samples. The differences among seedling means for FLUT and ASYM were not statistically significant among seedling grove samples after 29 growing seasons.

Mean crown fullness (FULL) was greatest in Cedar Flat seedlings at 138% (CV = 53%) of the seedling mean (Table 19). The crowns of Garfield seedlings ranked last at 60% (CV = 77%) of seedling mean FULL. Differences in FULL among seedling means were significantly different ($p \leq 0.1$) at alpha = 0.1. Shorter seedlings with lower height-diameter ratios tended to have crowns that scored highly in FULL according to correlations of FULL with HT ($r_s = -0.21$) and HDR ($r_s = -0.46$) among seedlings at FSO.

Epicormic sprouting (EPI) was highly variable among seedling grove samples after 29 growing seasons at FSO with a CV = 340%. Many individual SEGI seedlings had no epicormic sprouts as of 2009. One seedling grove sample, Giant Forest, had no

incidence of epicormic sprouting observed in 2009. The Garfield seedling grove samples had the greatest mean EPI at 196% of the seedling mean with a CV = 171% indicating great within-grove sample variability in this trait. All seedling grove samples had at least one individual that had no incidence of epicormic sprouting observed as of 2009. Differences among seedling grove samples were not statistically significant for this trait.

3.4.3 Trial 1 comparative performance and morphology of SEGI seedlings and stecklings

After 29 growing seasons at FSO, SEGI seedlings were larger than the SEGI stecklings in mean HT09, DBH09, and VOL09 with statistically significant differences for each trait (Figure 45, 46, and 47). Height differences between SEGI seedlings and stecklings were statistically significant in each measurement year except after the first growing season HT81 (Figure 45). A nursery effect may have confounded comparison of SEGI stecklings with seedlings.

There was a large and statistically significant difference in early mean relative height growth rate (RGRh83) of SEGI seedlings and stecklings. This difference in mean relative height growth rate of seedlings and stecklings was not present in the next two measurement periods RGRh88 and RGRh91 (Figure 48). This suggested that the difference in size of seedlings and stecklings after 29 growing seasons was largely influenced by the early difference in growth, possibly attributed to a short-lived nursery effect.

Following thinning in 1991, with the stecklings and seedlings still growing intermixed, RGRh97 of seedlings was significantly greater than that of stecklings for the period 1991 to 1997 (Figure 48). The taller seedlings were better able to take advantage

of the newly available growing space and increased their height advantage over the stecklings. The thinning in 1999 appeared to relieve competition among stecklings and seedlings for the growth period 1997 – 2009 because RGRh09 of the two stock types did not differ significantly (Figure 48).

Mean HDR09 of stecklings and seedlings were significantly different after 29 growing seasons ($p \leq 0.01$). In the two earlier measurement years, HDR91 and HDR97 did not differ significantly (Figure 49).

The SEGI planting stock types differed in form trait expression for mean FLUT ($p \leq 0.001$), FULL ($p \leq 0.001$), and EPI ($p \leq 0.0001$) after 29 growing seasons (Figure 50). There was no evidence of significant differences between seedlings and stecklings in SWEL. The North Calaveras seedling and steckling grove samples both exhibited large mean SWEL values with the seedlings exceeding the overall mean by ~15% more than the stecklings. The SEGI seedlings demonstrated greater mean ASYM at FSO than the stecklings, but this was not a significant difference (Figure 50).

The large difference in mean FLUT between the seedlings and stecklings was likely related to the difference in mean tree size between the larger seedlings and smaller stecklings. Larger trees expressed more FLUT at FSO with moderate significant correlations between FLUT and VOL09 ($r_s = 0.37$; $p \leq 0.001$).

Mean FULL was greater among SEGI stecklings than seedlings after 29 growing seasons and this difference was statistically significant ($p \leq 0.001$) (Figure 50). There was a negative correlation between FULL and HDR09 among SEGI seedlings ($r_s = -0.38$; $p \leq 0.001$) and stecklings ($r_s = -0.32$; $p \leq 0.001$) at FSO. This correlation indicated that

stockier trees at FSO carried more branches per stem length or larger branches with a bushier appearance than more slender trees.

Epicormic sprout formation was more frequent in SEGI stecklings after 29 growing seasons than in seedlings. Many individuals of both planting stock types did not have any epicormic sprouts in 2009. Only ~7% of the seedlings had epicormic sprouts, while 33% of the steckling sample trees had live epicormic sprouts at the time of assessment in 2009.

3.5 Performance of SEGI Seedlings in Trial 2 Mixed Conifer Planting over 29 Growing Seasons at FSO

3.5.1 Trial 2 SEGI seedling and mixed conifer seedling performance after 29 growing seasons

In the trial 2 mixed conifer planting at FSO, mean HT09 after 29 growing seasons of the six mixed conifer species was 15.5 m (s.d. = 4.8 m) (Table 20). The SEGI seedlings from the Garfield grove sample (hereafter referred to as SEGI seedlings) ranked fourth out of six mixed conifer species in mean HT09 at 14.7 m (s.d. = 3.9 m). Mean HT09 of PIPO, PILA, and PSME all exceeded the SEGI seedling mean by greater than 15%. Lagging behind these top four species were ABCO and CADE at 18% and 40% below the mixed conifer mean HT09 respectively. Differences among the mixed conifer species were highly statistically significant in an ANOVA of individual tree HT09 on species ($p \leq 0.0001$). Mean HT09 of PIPO ($p \leq 0.0001$) and PILA ($p \leq 0.0001$) were both significantly greater than SEGI mean HT09 in a multiple comparison test. Mean HT09 of

PIPO was significantly greater than HT09 of all other species in the planting. Mean SEGI HT09 was statistically significantly greater than CADE HT09 ($p \leq 0.0001$) in the same multiple comparison test. Mean HT09 of SEGI in this western block of trial 2 was greater than in the SEGI steckling block of trial 2 and greater than trial 1 seedling mean HT09.

Early growth in the mixed conifer planting was led by SEGI and CADE after three growing seasons at FSO. In HT83, SEGI and CADE were the only species with mean HT83 greater than the mixed conifer mean at 157% and 123% respectively (Table 20; Figure 51). The first three growing seasons at FSO experienced the greatest annual precipitation at FSO of the 29 growing seasons of the trials. This three year period experienced mean annual precipitation 600 mm above the long term annual mean of 1300 mm at FSO, with 1982 and 1983 the two wettest years in the life of trials exceeding 2000 mm in each year.

After six growing seasons, PIPO mean HT86 was 111% of the mean while SEGI and CADE continued to rank first and second respectively, though both no longer outsized the other species by such large margins (Figure 51). The wet years from 1981-1983 were followed by seven years from 1984 to 1991 which were the driest in the life of the trials. In this period, the pines performed relatively better than SEGI and CADE. Mean annual precipitation at FSO in these years averaged 200 mm below the long term mean (Figure 52). At the next measurement period in 1991, SEGI HT91 was 115% of the mean and CADE mean HT91 was 10% below the mean. Mean HT91 of PIPO was greater than the SEGI mean at 129% of the mixed conifer mean. In this measurement year, mean HT91 of PIPO and SEGI were significantly greater than the other four conifer species in

a multiple comparison test. By 1997, PIPO mean HT97 was significantly greater than SEGI mean HT97 ($p \leq 0.0001$). In this year, both PILA and PSME were taller than SEGI (Table 20; Figure 51).

Mean DBH09 in the mixed conifer planting of trial 2 was 32.1 cm (s.d. = 11.7 cm) after 29 growing seasons in 2009 (Table 21). As of 2009, SEGI seedling mean DBH09 was below the mixed conifer mean and ranked fourth behind PIPO, PILA, and PSME (Table 21). The trend in DBH from the 11th growing season to the 29th paralleled the trend in HT for this same time period. The pines and PSME gradually overtook SEGI in DBH. These same trends describe the changes in VOL from the 11th to 29th growing season as well. By 2009, PIPO VOL09 was 200% of the mixed conifer mean and 70% larger than the second-ranked PILA (Table 22).

Mean relative height growth rates differed among species for each measurement period (Figure 53). The pines dominated the dry period from 1984 to 1986 with RGRh86 of PILA and PIPO at 118% and 114% of the mixed conifer mean respectively (Figure 53). For the most recent measurement period from 1997 to 2009, ABCO had the highest RGRh09 (0.092 m m^{-1} yr^{-1}; s.d. = 0.005 m m^{-1} yr^{-1}) of 44% above the mean with PILA ranked second in RGRh09 (Figure 53). At this time, PSME grew at an above average relative height growth rate, while SEGI and PIPO lagged with relative height growth rates below the mean (Figure 53).

Mean height-diameter ratio (HDR) of the mixed conifer species was increasing as of the 29th growing season in the mixed species planting of trial 2 (Table 23). Mean HDR09 was 50 (s.d. = 6.8) compared to mean HDR97 of 43 (s.d. = 12.3), a likely

indication that the stand was becoming crowded and stem diameter growth was restricted by competition. Mean HDR09 was increasing for PIPO and SEGI, but decreasing for all other species (Table 23). The slow growing ABCO had the highest HDR09 at 63 (s.d. = 4.5) having decreased from 105 at the approximate time of crown closure in 1991.

3.5.2 Competitive effects of mixed conifer neighbors on SEGI seedling growth

A nearest neighbor analysis investigated various competition indices for modelling SEGI diameter growth increment (DINC mm) from 1997 to 2009 as a response to neighborhood mixed conifer competition in neighborhoods varying from 5 m to 11 m in radius. The best fitting competition index (CI) of total neighborhood mixed conifer competition by information criterion selection method (AICc) was a 7 m neighborhood incorporating neighbor tree DBH^2 relative to SEGI subject tree DBH^2 scaled for distance in meters from subject tree to neighbor tree and log-transformed ($lnCIdbh^2$) (Table 24). The log-transformed CI was a better fit of the data linearizing some curvature in the residuals of the un-transformed model. This model had lowest AICc of 173.96 and Akaike weight of 0.38 indicating a 38% likelihood that this model was the best model of the candidate set of models analyzed. An adjusted-R^2 of 0.64 indicated a strong relationship between the explanatory CI and SEGI DINC and supported this model as a good fitting model of SEGI DINC (Table 24).

Two other CI models were within three ΔAICc of this best model indicating that they were statistically viable models of SEGI DINC (Burnham and Anderson 2002). The log-transformed $CIdbh^2$ at 10 m had an AICc value within 0.1 of the best fitting CI and Akaike weight of 0.36 indicating a comparable likelihood that this larger neighborhood

radius may be the best model of SEGI DINC (Table 24). The log-transformed Hegyi index lnCIHeg at 7 m was within one point of the best model AICc with a weaker Akaike weight of 0.22 (Table 24). All three of these models were better fits of SEGI DINC by AICc than 7 m neighborhood basal area (BA m^2) (AICc = 208.3) and 7 m stand density index (SDI) (AICc = 216.9) or 10 m basal area (AICc = 215.47) and 10 m SDI (AICc = 216.53).

The effect of individual species neighborhood CI on SEGI DINC was investigated for the six mixed conifer species, including SEGI, competing with SEGI seedlings in trial 2. The full model included an explanatory variable for the sum of the species CI for each competing species present within a SEGI subject tree 7 m radius neighborhood. The best model was selected using a stepwise regression procedure by AICc. This stepwise procedure was done for the full species models in 7 m neighborhoods for lnCIdbh^2 and lnCIHeg. The best fitting model by AICc selection method included lnCIHeg values for competing species SEGI, PIPO, ABCO, and CADE, leaving out PILA and PSME competition (Table 25). The Akaike weight of this model (0.34) indicates a 34% likelihood that this model was the best model of SEGI DINC of the candidate models (Table 25). The adjusted-R^2 of 0.65 also indicated a good fit for this model of SEGI neighborhood competition by species. The model including PSME CI had a higher adjusted-R^2 at 0.66 and was within one point of AICc from the best model suggesting statistical viability and goodness of fit. The Akaike weight of this model with PSME CI (0.21) indicated a 21% likelihood that this was the best fitting model (Table 25.

All models of mixed conifer species neighborhood competition on SEGI DINC that included PILA CI had ΔAICc > 3 and Akaike weight < 0.05. The removal of PILA CI thus improved the model of SEGI DINC by a statistically significant margin (Burnham and Anderson 2002). This suggested that PILA was not a significant source of competition on SEGI diameter increment growth at FSO from 1997 to 2009. It should be noted that this result was not likely the result of low vigor of PILA neighbors during this growth period. *Pinus lambertiana* were the second largest species by mean HT09, DBH09, and VOL09 and had the second highest relative height growth rate (RGRh09) for the period, while SEGI seedlings were growing slower than the mean (Figure 53).

3.6 Effects of Mixed Conifer and Brush Competition on SEGI Growth in Trial 3 after 29 Growing Seasons

After 29 growing seasons at FSO, SEGI ranked fifth of the six mixed conifer species across all treatments in the trial 3 brush competition planting in HT09, just below ABCO (Table 26). In DBH09 and VOL09, SEGI ranked fourth at 90% and 64% of the trial mean respectively (Table 26). The two pine species, PIPO and PILA, demonstrated the best performance in the trial, with PIPO outgrowing PILA by 25% in VOL09. Behind the pines, but ahead of SEGI by a substantial margin was PSME at 120% of trial mean VOL09. At the bottom of the VOL09 ranks, ABCO and CADE lagged behind with poor VOL09 performance of 60% and 4% of the trial mean respectively (Table 26). Mean HDR09 of SEGI seedlings (58.5) was greater than HDR09 of PIPO and PILA (Table 26).

Though the overall performance of SEGI seedlings was poor in trial 3, the largest single tree in the trial was a SEGI in an edge location on the north side of the trial at 1.64 m^3.

Growth differed significantly among species and among brush treatments in trial 3 after 29 growing seasons (Table 27). Species and treatment were highly significant ($p \leq 0.0001$) for the response VOL09, as were their interaction ($p \leq 0.001$). Edge location was marginally significant ($p = 0.05$) but the interaction of species and edge ($p \leq 0.0001$) was highly significant so edge was necessarily included in the model. Effect slices for species × treatment indicated that treatment was highly significant for the two pine species ($p \leq 0.001$), significant for PSME ($p \leq 0.05$), and marginally significant for SEGI ($p = 0.09$) (Table 28). All conifers performed better on bare ground than with either brush type, except for PSME, which had greater VOL09 in the *manz* treatment (Figure 54).

The multiple comparison test of significance of treatment within species (Figure 54) demonstrated that mean VOL09 of SEGI seedlings in the *cean* treatment did not differ from either *bare* or *manz* treatments. Mean SEGI VOL09 was lower in the *manz* treatment than the *bare* treatment ($p \leq 0.05$). For both of the pine species, VOL09 was greater in the *bare* treatment than both brush treatments, which did not differ from each other. For PSME VOL09, the *manz* and *bare* treatments did not differ, but were both significantly different from the *cean* treatment. There were no significant differences among treatments for ABCO or CADE VOL09 after 29 growing seasons.

3.7 Heartwood Decay Resistance in SEGI Stumps Thinned in 1999

In stumps of SEGI seedling grove samples thinned in trial 1 in 1999, there was little variation in mean heartwood decay resistance (Table 29). The seedling grove sample with the largest mean decay resistance and the lowest mean decay resistance differed by only 12%. Most of the grove samples had mean decay resistance scores near or greater than two on a four point scale indicating that thinned stumps had generally sound heartwood as of 2010. It may be that insufficient time has passed to produce substantial decay in the heartwood of SEGI. Tree size was investigated for a relationship with heartwood decay resistance hypothesizing that larger trees would produce more decay resistant heartwood but correlations and regression indicated no evidence of a relationship.

In stumps of SEGI standard clones thinned in 1999, heartwood decay resistance was more variable than among seedlings. Heartwood decay resistance was greatest on average in standard clones in the Mountain Home grove sample (Table 30; Figure 55) in 2010 eleven years after thinning in 1999. The stumps of three standard clone grove samples had above average heartwood decay resistance: North Calaveras, Cedar Flat 2, and Mountain Home (Figure 55). Two of these standard clone grove samples with above average decay resistance originated in small area native groves, the stecklings of which performed poorly in tree size traits over 29 growing seasons. The other, Mountain Home, was a large area grove sample and the Mountain Home stecklings were largest by tree size traits at FSO. However, variability in decay resistance was high and differences in heartwood decay resistance were not significant among the stumps of standard clones from eight grove samples thinned in 1999 ($p = 0.47$; Table 30; Figure 54).

In analysis of the heartwood decay resistance of standard clone stumps thinned in 1999, region of clone origin in the native range was a significant explanatory variable ($p \leq 0.05$) (Figure 56). Heartwood decay resistance was greatest at FSO in the thinned stumps of standard clones with origins in the south region of the native range, which were significantly different from north region stumps in a multiple comparison test ($p \leq 0.05$) (Figure 56). Mean DBH of standard clones in 1997 two years before thinning was included in the analysis to account for the effect of size differences in the cut stumps on heartwood decay resistance. The covariate for DBH97 was not significant ($p = 0.39$) in this analysis.

4. DISCUSSION

4.1 Population Variation of SEGI Stecklings at FSO over 29 Growing Seasons

After 29 growing seasons at FSO, SEGI stecklings were generally expressing more genetic variation in size and form traits among-clones, among-groves, and among-regions than at any time during the life of the trials. Genetic variance estimates were higher than expected for SEGI tree size traits and were moderate to high for both SEGI size and form traits.

At this site north of the current native range of SEGI, trees from the south and central region grove samples grew significantly better than SEGI from the north region grove samples. However, the strongest predictor of tree size at FSO was the area of native grove origin which was positively associated with mean SEGI HT09 after 29 growing seasons. There was variation between the two trials at FSO, but the same grove samples had the largest mean HT09, DBH09, and VOL09 in both trial 1 and 2: Mountain Home, Converse Basin, and Giant Forest. All three of these grove samples originated in the central and south regions of the native range and were large groves by area. (The discussion of the analysis of geographic characteristics is found in section 4.2).

4.1.1 Among-clone variance in SEGI steckling tree size and form traits after 29 growing seasons

The among-clone variance was an estimate of rangewide genetic variation broad-sense heritability (H^2) for these size and form traits at age 29. These are the first such

estimates of genetic variation in SEGI size and form traits at this age and should be interpreted with caution given that they are based on a small sample of clones (trial 1, n = 50; trial 2, n = 17) and were derived from a single site, which likely inflates heritability estimates (White et al. 2007). The estimates in both trials were based only on data for trees surviving and eligible as of 2009. Available data for additional trees from past measurement years were not used in this analysis. This omission of additional data may have resulted in more conservative estimates of variance components and heritabilities in this analysis. It is important to note that the clones available for analysis in trial 1 and trial 2 were not identical replication of clones. They were from the same seed collection and propagated in the same nursery, but only two clones appear in both trials as of 2009 due to differential survival and thinning within the trials. There are relatively few studies estimating rangewide genetic variances for forest trees (broad-sense heritability, H^2) due to the need for clonally propagated field plantings from rangewide seed collections. The demand for land and time has made these types of experimental plantings rare.

At age 29, rangewide genetic variance in SEGI HT09, an estimate of the total contribution of genetic variation within the species for this trait, accounted for 47% of total phenotypic variation in both trial 1 and trial 2 at FSO (H^2 = 0.47). The genetic variance in HT was higher than expected, particularly given SEGI's low levels of genetic variability by genome size and heterozygosity (Ahuja 2008, Fins and Libby 1982, Fins and Libby 1994). In clonal studies of *Picea abies*, median broad-sense heritability for HT was 0.17 (Rosvaal et al. 2001 cited in Hannrup et al. 2004), but was as high as 0.54 at age 19 from a single site estimate (Hannrup et al. 2004). There are estimates of genetic

variance in growth for other Sierra conifers that are comparable to the SEGI estimates. In common-garden trials in CA and OR, 40% of the variability in PILA growth was attributed to genetic sources of variation (Kitzmiller 2004).

The higher than expected genetic variance estimates may be the result of the relatively homogenous environmental conditions within each trial. Genetic variances tend to be high when environmental variability is stable reducing the environmental component of variation within the trial (White et al. 2007). The FSO planting site was cleared of all brush and root systems prior to planting and both trials have been kept free of invading shrubs and herbaceous species by the USFS throughout the life of the plantings. On more heterogenous sites on which site preparation has not been as intensive, I would expect heritability of SEGI HT to be lower than it was at FSO.

Alternatively, the higher than expected genetic variance estimates may be due to certain clones reacting more favorably to the clonal propagation methods used to produce the rooted cuttings, called C-effects (White et al. 2007). These C-effects inflate the variance among-clones, upwardly biasing the genetic variance estimates and may persist for various lengths of time (Libby and Jund 1962 cited in White et al. 2007, Burdon and Shelbourne 1974 cited in White et al. 2007, Foster et al. 1984).

If inbreeding were occurring within some of the sampled SEGI native groves, variation among individuals within these populations could be reduced thus upwardly biasing the estimates of genetic variance (Sorensen and White 1988). Inbreeding as a potential source of upward bias in the genetic variance estimates can be ruled out based on results from analysis of microsatellite loci of SEGI from the same rangewide seed

collection planted in a clonal orchard at U.C. Russell Research Station. These results indicated that inbreeding was not occurring in the grove samples included in my analysis (Dodd and DeSilva 2016).

Among-clone variance in SEGI with advancing age. Genetic variance in SEGI HT generally was larger with advancing age among-clones over 29 growing seasons. There is little agreement in the literature on whether genetic variance in height of tree species is expected to increase or decrease with advancing age. Increases in genetic variance in height with age may be explained by a decrease in environmental variation within a stand as trees grow larger and sample a larger microsite area both aboveground and belowground. As trees expand their crowns and root systems within a stand, they sample a larger microsite area thus reducing the variation within a stand due to differences in microsite quality. This will have the effect of reducing the residual error variation, which in an ANOVA among-clones can be interpreted as variation due to environmental factors. Or, as competition in a stand increases with age, the increased crowding will result in rapid differentiation of strong genotypes and weak genotypes thus increasing the variance among the genotypes. (Namkoong et al. 1972, Namkoong and Conkle 1976, Franklin 1979). Genetic variances in height that have decreased or been constant with advancing age have been attributed to the random effects of variable competition levels within stands. When one ramet of a clone has a weak neighbor and another a more competitive neighbor, the variability within clones will increase due to their differential growth thus lowering genetic variance (Bouvet et al. 2003, Brouard and John 2000, Farmer et al. 1993, Haapanen 2001, Kroon et al. 2011).

The lowest genetic variance occurred in SEGI HT88 at 7% which was prior to crown closure in the pure-SEGI planting of trial 1. At this time the individual trees were free to grow without competition from neighboring trees, but had been on site long enough that their root systems had become well-established. This freedom to grow likely resulted in a period of more uniform growth among individuals following earlier strong differences in height while trees were still establishing root systems, thus reducing variation among-clones within the stand and genetic variance in HT88.

At the next measurement in 1991, genetic variance in HT91 was larger at ~17% of phenotypic variance, all of it occurring among-clones. It is likely that this was related to an increase in competition among trees as the site became fully occupied as of 1991 (W.J. Libby, pers. comm.). Certain clones may have responded better to the more competitive growing environment. More competitive clones differentiating from less competitive clones would cause larger variance among-clones. Similar results were seen in a common-garden study of ponderosa pine (PIPO) when in the 20^{th} year on site family variance increased as the site became more crowded (Namkoong and Conkle 1976). The increase in family variance was attributed to the adaptation of certain families to competition for late growing season soil moisture in the more competitive environment.

Following thinning of the trial in 1991, genetic variance was larger in 1997 and 2009. All genetic variance in HT97 was found among-clones. This may be an indication that following thinning, the superior clones continued to increase in height and separate themselves from slower growing clones. These differences in HT97 may have been related to differences among clones in adaptiveness to drought conditions during the

years 1984 to 1991 in which mean annual precipitation was below the 30 year average at FSO. However, mean annual precipitation during the subsequent wetter than average period from 1991 to 1997 was not significantly different from the previous dry years at FSO (Figure 52).

Genetic variance in HT09 was the highest it had been over the life of the trial with most of it occurring among-clones (33%). Among-region variance (15%) was a significant source of variation, with clones from the north region significantly shorter than trees in the south region. As trial 1 aged, these regional differences in height had become stronger suggesting that there may be genetic differences in HT growth among-regions within the SEGI native range. It will be interesting to see if the genetic variance in SEGI height will be greater in the next measurement year in trial 1 or if among-clone variance will begin to decline as the tallest clones slow their growth as they mature with advancing age.

In the mixed species planting trial 2, the trends in genetic variance in SEGI height differed from trial 1 with stronger genetic variances expressed at an earlier age. There was no genetic variance in HT81 as trees became established on site. Genetic variance peaked in trial 2 HT83 (36%). The genetic variance in HT83 was strongest among-clones (26%) with 10% of the variation occurring among-regions as the north region clones lagged behind the central and south region clones (Table 10).

Genetic variance in trial 2 HT83 (36%) was larger than in trial 1 (17%). It was difficult to explain why genetic variances were higher in trial 2 at this time. Trees were not competing with each other so the high genetic variance was likely not related to

competitive factors with mixed species neighbors. Genetic variance and heritability may be better expressed on more productive sites at earlier ages (Namkoong et al. 1972). Trial 2 does slope gently to the west of trial 1 and it may be that soil moisture or nutrients accumulated along this slope making trial 2 a more productive site. Mean clone HT83 in trial 2 (0.87 m) was greater than in trial 1 (0.84). The trial 2 central and south clones in particular were ~ 0.1 m taller than the trial 1 clones respectively. This large difference in HT83 between the trials suggested that the better site quality of trial 2 could be driving the higher genetic variance in trial 2. The higher genetic variances in trial 2 may be a result of the the small sample size of clones producing large standard errors of the variance estimates (not shown).

Genetic variance in trial 2 HT continued to increase with age. It was high at age 8 (44%), which was the age when genetic variance in trial 1 (2%) was lowest, and at age 11 when crowns were closing in both trials and competition was likely greatest. The high genetic variance at this time in trial 2 was dominated by among-region variance in contrast to trial 1 which was all among-clone variance. The central and south region clones in trial 2 continued to extend HT differences with the north region clones.

Among-clone variance in trial 2 was lower in HT91 (7%) at the time of crown closure than in HT88 (13%) when genetic variance was lowest in trial 1. This could be related to differential levels of competition with mixed conifer neighbors leading to increased variation within-clones dependent on species composition of nearest neighbors. The CADE and ABCO individuals were generally smaller than PIPO, PILA, or PSME neighbors. The increase in among-region variance may be indicative of the greater

competitive ability of central and south groves. Or the greater competition may be causing more rapid differentiation among the poor growing north region SEGI trees and the better performing central and south region trees. Following the thinning in 1991, trial 2 genetic variance in HT97 remained at 7% of phenotypic variance. The regional variance was lower in HT97 possibly due to north region trees catching up to the superior central and south region SEGI as growing space became available following thinning.

Among-clone variance in SEGI diameter and volume. The genetic variance for SEGI DBH and VOL in trial 1 and 2 followed generally the same trend as genetic variance in HT, increasing with advancing age from 1991 to 2009. The genetic variances for DBH and VOL were only slightly lower than HT, which has been observed in several species (Burdon 1965, Bouvet et al. 2003). This may be due to the greater sensitivity of DBH and VOL to competition and growing space resulting in larger environmental variance for these traits (Burdon 1965).

As observed for genetic variance in HT, genetic variance in DBH and VOL were higher in trial 2 than in trial 1. This may be due to site productivity of trial 2 leading to earlier differentiation of the larger central and south region clones from the smaller north clones. The most notable difference in variance between the two trials was that all of the genetic variance in trial 2 occurred among-regions with no variance occurring among-clones. In trial 1 most of the genetic variance occurred among-clones, though the among-region variance was larger in 2009 than at any time during the life of the trials. The less uniform growing conditions in the mixed species planting of trial 2 due to the presence of

highly variable sizes of mixed conifer neighbors likely increased within-clone variability in trial 2.

Among-clone variance in SEGI height-diameter ratio. Genetic variance was high for HDR at FSO after 29 growing seasons with 52%-80% of the phenotypic variation explained by genetic sources. This was the highest genetic variance of any trait assessed at FSO. This was evidence of strong genetic control of this trait in SEGI. In both trials, nearly all of the genetic variance in HDR occurred among-clones suggesting that this trait was highly heritable and could be part of a tree improvement program. However, HDR was moderately positively correlated with VOL ($r_s = 0.33$) at FSO, with some of the largest trees by VOL with low HDR and some of the smallest trees with the high HDR. A positive correlation between HDR and wood stiffness has been observed in other species (Kijidani et al. 2010, Waghorn et al. 2007). If a similar relationship exists for SEGI, then HDR could be an important trait for selecting trees for timber utilization.

Among-clone variance in SEGI stem form traits. Among-clone variance was generally higher for the SEGI stem-form traits at FSO than the tree size traits, with the exception of fluting of the lower stem (FLUT). It is thought that form traits are under greater genetic control than growth traits, but the evidence for this has not been conclusive (Cornelius 1994). Based on Fisher's Fundamental Theorem of Natural Selection (1930), traits that are strongly related to an organism's overall fitness, such as height, are hypothesized to display lower genetic variance and thus lower heritability (Falconer and Mackay, 1996). The theory postulates that natural selection will act strongly on a trait that is strongly related to fitness, thus reducing the overall genetic

variability in this trait over many generations. Traits less related to overall fitness such as branching characteristics and stem form may be under strong genetic control. In both trials at FSO, the SEGI form traits with the highest genetic variances were crown fullness (FULL) and basal swelling (SWEL). In trial 1, all genetic variance in stem form traits was clonal variance, while in trial 2 most of the genetic variance occurred among-regions (Table 11).

The FLUT trait had negative values for clonal variance suggesting either a strong environmental influence on this trait or a widespread genetic trait of the species as has been suggested by results from SEGI plantings in New Zealand (L.E. Freer, unpublished data). The strong relationship of fluting to size of SEGI at FSO may be a warning to land managers interested in SEGI for wood production. In western hemlock (TSHE) fluting tended to initiate when growth rates increased (Julin et al., 1993b). How much of a concern this should be for SEGI depends on how the fluting response may change with DBH growth in subsequent years on site at FSO. It also depends on the length of timber rotations for SEGI grown for wood production. Fluting of TSHE tended to increase with age until leveling off at some point in time when radial growth within flutes increased, possibly due to branches breaking off (Julin et al., 1993b). These findings suggest that SEGI may eventually grow out of this fluting as growth rates decline with advancing tree age and increasing stand density at FSO. If SEGI fluting is temporary and corrects itself before rotation age, then fluting may pose very little problem from a timber perspective. Fluting should be monitored at FSO with attention to trends in growth rate and initiation and cessation of fluting investigated.

Epicormic sprouting in trial 2 had a negative clonal variance, while in trial 1 20% of variance occurred among-clones. Epicormic sprout formation was relatively infrequent in both trials. Only young epicormic sprouts were assessed at FSO in 2009. The last thinning had occurred in 1999 and trial 2 was generally more crowded than trial 1. If light was more limited in trial 2, it may be likely that only this random subset of trees would be more inclined to sprout epicormically if they happened to be exposed to light from thinning or mortality of neighboring trees. Trees not in a gap which remained in areas of lower light conditions may be less likely to form epicormic sprouts.

4.1.2 Among-grove variance in SEGI tree size traits after 29 growing seasons

Variation in size and form traits among-populations of forest trees has been generally smaller than variation within-populations for species with widespread ranges. This suggests that in most widespread species' ranges there has been substantial gene flow among-populations. This has strong support for population variation in widespread species when assessed by allozyme markers (Hamrick et al. 1981, Hamrick et al. 1992). Tree species with disjunct distributions of isolated populations, such as SEGI, may be expected to possess greater variation among-populations than widespread tree species depending on the degree of population isolation and the time since isolation has occurred. The quantitative genetic analysis of SEGI traits at FSO demonstrated several instances of statistically significant genetic variation among-groves including DBH09, VOL09, HDR09, SWEL, FULL, and EPI (Table 11). In all of these instances, the residual variance, which included the within-grove variance, was greater than the among-grove variance. This suggested that variation among individuals within grove samples may have

been greater than the variation among groves as was the case for most tree species. The confounding of within-grove variance with residual variance in this analysis may be due to the lack of adequate clonal replication within grove samples in both trials. This was a limitation of this analysis and prevented greater certainty in the comparison of among-grove and within-grove levels of variation in SEGI traits. Additionally, the large among-trial variance in this analysis in HDR09, SWEL, FULL, and EPI may have reduced the magnitude of the among-grove variation detected in these traits.

In two traits, DBH09 and VOL09, among-grove variation was greater than the among-region estimate of variation (Table 11), suggesting that in these traits certain native groves may be better adapted for rapid diameter and volume growth. Based on this result, it will be important for future seed collections with the objective of producing propagules with rapid diameter and volume growth to collect seed within specific native groves exhibiting these traits rather than specific regions. This among-grove variation in DBH09 and VOL09 at FSO was largely influenced by the performance of the Mountain Home grove samples. In both trials, the same three grove samples had the largest DBH09 and VOL09 rankings: Mountain Home, Converse Basin, and Giant Forest. All statistically significant differences among-grove samples in multiple comparisons tests for DBH09 and VOL09 involved the Mountain Home grove samples being significantly greater than several grove samples from throughout the range. Seed collection from this native grove, as well as Converse Basin and Giant Forest, home to the largest individual tree by volume, General Sherman, should make good sources of future seed collections for outplantings for which prioritizing SEGI volume growth will be a primary objective.

The lack of strong evidence for variation among-groves in SEGI traits may be an indication that SEGI groves have become isolated relatively recently. It is not known when or how the disjunct SEGI populations became isolated. There is evidence of SEGI populations both east of the Sierra Nevada and at lower elevations within the current species range along the west slope of the Sierra Nevada within the last 10,000 years (Anderson 1994, Axelrod 1959, Davis 1999, Davis and Moratto 1988). Evidence from palynological studies in Log Meadow within Giant Forest grove, suggest that SEGI has been present in this location for only ~ 4000 years (Anderson 1994). Given SEGI's potential lifespan of several millennia, this may be only two generations, a relatively short timespan for genetic divergence of populations to occur. It is possible that many of the current SEGI populations may be relatively recent arrivals in their current habitat, having migrated from lower elevations in response to changing climate or other environmental conditions. However, there has been no evidence suggesting the more disjunct SEGI populations, as in the north region, were once more continuous along the west slope of the Sierra Nevada (Rundel 1971, 1972). Large population differences have been found in common-garden trials of the five widely disjunct native populations of *Pinus radiata* (Burdon et al. 1992, Raymond and Henson 2009). The *P. radiata* populations are generally smaller and more isolated, separated by as much as several hundred miles, than the SEGI groves. The greatest distance among native SEGI groves is approximately 80 km, between the northernmost Placer Grove and North Calaveras Grove.

The estimates of genetic variation in size traits from the combined single-ramet trial 1 and trial 2 data at FSO were lower than the estimates from the among-clone analysis, varying from 13% in HT09 to 34% in VOL09. This result differs from the estimate of genetic variance among-clones in which HT09 had higher levels of genetic variation than DBH09 or VOL09. The total amount of genetic variation in this among-grove analysis was more in line with expectations of lower levels of genetic variance in SEGI traits. These quantitative estimates of SEGI among-grove genetic variance in HT09 at 13% was comparable to the 10% genetic variation among-groves and 90% within populations reported from isozyme analysis (Fins and Libby 1982). The reported 10% among-grove variation in SEGI by isozyme variability was slightly above average for gymnosperms where the reported average was 7% among-populations (Hamrick et al. 1992). Reports of quantitative genetic variation are often much higher than this in woody species with widespread ranges. As an example, *Pinus contorta*, a widespread gymnosperm with several ecological varieties, had 38% of variation in quantitative traits estimated among-populations while only 6% of isozyme variation was found among-populations (Wheeler and Guries 1982). There has been little agreement between estimates of genetic variance for isozyme traits compared to quantitative traits like height because isozymes may not respond to selection pressure in the way phenotypic traits do (Bergmann 1978, Yeh et al. 1985, Muller-Starck et al. 1992).

Among-grove variance in SEGI stem form traits. There was small, but statistically significant among-grove variation in basal swelling (SWEL), crown fullness (FULL), and epicormic sprouting (EPI) at FSO after 29 growing seasons. This suggested that these

traits may be genetic traits of certain native SEGI groves. While among-grove variation was strongest for EPI with ~7% of the phenotypic variation found at this level, there were no significant differences among individual groves in multiple comparisons tests. Generally, grove samples in the south region expressed the most EPI including Cedar Flat/South Fork and Packsaddle. In FULL, the North and South Calaveras grove samples generally had more full crowns, but did not differ significantly from individual grove samples.

In mean SWEL, the North Calaveras grove sample had high levels of mean SWEL in both trial 1 and 2 as well as among SEGI seedling grove samples at FSO. This native grove was the source of many of the SEGI planted in Europe where basal swelling had been noted as a prominent trait (W.J. Libby, pers. comm.). Since many of the SEGI trees were planted in parks and were open-grown it has been thought that the basal swelling observed in these trees may have been a response to the environmental influence of open growth. These results from FSO suggest that basal swelling may be a genetic trait of the North Calaveras grove. There were significant differences in basal swelling between North Calaveras and Packsaddle grove samples, the southernmost grove sample in this analysis which had significantly less basal swelling. Caution must be exercised in the interpretation of this significant among-grove variation in SWEL. The Black Mountain 1 and 2 grove samples demonstrated contrasting trends in this trait in the two trials. Since both grove samples originated in the same native grove, this may indicate a spurious among-grove significance in this trait.

4.1.3 Among-region variation in size and form traits over 29 growing seasons

Among-region differences were prominent for tree size traits after 29 growing seasons at FSO explaining 10% of the phenotypic variation in HT09 and 15% in VOL09. At this site north of SEGI's native range, SEGI stecklings from the central and south region grove samples were taller and larger than the north region grove samples. This was contrary to the expectation that as provenance trials age the more local populations have tended to perform relatively better in comparison to more distant populations (Millar and Libby 1989).

Regional trends in SEGI tree size traits have not been conclusive in other SEGI provenance trials. Results similar to those at FSO were observed in German provenance trials with SEGI planted at latitudes far north of the current native range (>51° N). Two central and south groves, Whitaker's Forest part of Redwood Mountain grove and Mountain Home, had the largest average heights at age 12 (Dekker-Robertson and Svolba 1991). In SEGI plantings at age 26 in New Zealand (45° S) from eight provenances, including Whitaker's Forest and Mountain Home, two north region grove samples, Nelder and North Calaveras, demonstrated the best growth performance (De La Mare, 2004). This relationship between better growth in provenances from more southern latitudes has been demonstrated in species with wider latitudinal ranges than SEGI, including *Juniperus virginiana* (Henderson et al. 1979), *Pinus strobus* (Wright 1970), and *Podocarpus totara* (Bergin et al. 2008). In these species it was thought that smaller but hardier genotypes were better adapted to the colder latitudes, while genotypes from the more mesic latitudes would be selected for rapid height growth.

Another possible explanation of this better performance of the south region grove samples at FSO and in Germany may be adaptation to regional differences in photoperiod resulting in an earlier start to the growing season or a longer growing season for SEGI from south region groves samples when planted at more northern latitudes. This has been seen in provenance trials of PIPO in which growth of progeny was directly related to duration of growing period which corresponded with that of their native origin (Kitzmiller 2005). Progeny from the southernmost, mid-elevation sources grew best at a more northern site (Kitzmiller 2005). The south region grove samples may begin the growing season earlier than the trees from the north region. Investigation of variation in the length of growing season among SEGI at FSO could help explain the regional differences in growth. However, it is difficult to determine the length of growing season in SEGI since they do not set a terminal bud (Weatherspoon 1990).

The southern SEGI native groves have been characterized as drier and warmer than the northern groves (Raven and Axelrod 1978). Daymet data indicates cooler mean growing season temperatures with lower mean growing season precipitation than the north region native groves and the FSO study site (Table 2). There was discrepancy between the elevations from the Daymet output and the native grove data, so these climate means for the south region native groves may be subject to error. The SEGI stecklings from these southern grove samples may be better adapted to the warm, relatively dry growing site at FSO (Table 2).

In earlier isozyme analysis of the SEGI propagules from which the FSO trials were derived, genetic diversity as measured by heterozygosity increased clinally from

north to south in the grove samples (Fins and Libby 1982). To investigate whether quantitative genetic variance by region parallels isozyme variability in the FSO propagules, a variance components analysis among-clones was conducted independently by region. The clonal variance components were largest within the south region clones in both trial 1 and trial 2, paralleling the results of the isozyme analysis (data not reported). Clonal variance was lowest in the north region grove samples. Sample sizes were small and standard errors were large within each region. It should be noted that high levels of genetic variation are not necessarily strongly correlated with growth performance. At FSO the grove samples originating at the northern and southern range limits, the tiny Placer and Deer Creek grove samples, both performed poorly at FSO. The most local native grove, Placer Grove is known to be inbred with only six mature trees, while Deer Creek grove sample had a below average heterozygosity level (Fins and Libby 1982).

There is further evidence from earlier isozyme analysis indicating that the north region populations may be genetically distinct from the central and south region populations. In the isozyme analysis, the northern grove samples had the presence of the GOTc allele which was lacking from the central/southern populations (Fins and Libby 1982). This absence of this allele suggested that there had been little to no gene flow between the eight north region native groves and the more geographically continuous central/south region groves for some time (Fins and Libby 1982). It remains unknown whether northern and southern native SEGI groves migrated to their present locations from different origin populations or if the northern groves became isolated from the main population at some point in SEGI's evolutionary past. Both the quantitative genetic

analysis of SEGI traits after 29 growing seasons at FSO and the previous isozyme analysis of the same seed collection agree that the north region SEGI grove samples appear to be genetically distinct from the central/south region grove samples. Recent evidence suggests the northern and central/south populations diverged in the late Pleistocene (~ 2.3 Mya) due to a reduction in population size in the northern populations (Dodd and DeSilva 2016). The northern populations concurrently diverged into four genetically similar populations so that the current SEGI range may be divided into five distinct groups (Dodd and DeSilva 2016). Future field tests should focus on quantitative analysis of differences in tree-size and form traits among progeny from these five groups.

Among-region variation in SEGI epicormic sprouting. Among-region variation was detected in epicormic sprouting of SEGI stecklings at FSO, accounting for 6% of the phenotypic variance in this trait. There was greater incidence of epicormic sprouting in SEGI stecklings from south region groves. This regional trend of increasing epicormic sprouting from north to south was noted in the early analysis of the SEGI propagules used to establish the FSO trials (Fins and Libby 1982). Mean grove sample epicormic sprouting was also significantly correlated with mean grove sample heterozygosity by previous isozyme analysis. This suggested that the increased levels of epicormic sprouting in the south region grove samples may have been related to their greater genetic diversity.

4.1.4 Growth and tree size in pure SEGI vs. mixed planting at FSO

Information on SEGI growth and form traits in pure and mixed species plantings will help guide SEGI outplanting strategies for conservation and timber utilization. It is

likely SEGI will be planted on timberlands in California with other commercial Sierra conifer species, such as PIPO and PSME (Kitzmiller and Lunak 2012). In trial 2 at FSO, SEGI stecklings were planted with five Sierra Nevada conifer species: ABCO, CADE, PIPO, PILA, and PSME. Comparing growth of SEGI stecklings in the mixed species planting of trial 2 with growth of SEGI in the pure-SEGI planting of trial 1 alerts land managers to differences in growth or form traits in these different planting mixtures.

The SEGI stecklings in the two trials differed primarily in tree HT. Mean tree HT in trial 2 was statistically significantly greater than trial 1 in each measurement year from age 11 in 1991 to age 29 in 2009. The difference in mean HT in the two trials may be related to an environmental gradient in which trial 2 slopes gently westward and it is apparent that tree HT increases downslope along this gradient. Trees in both trials have their leaders at about the same level in the canopy as the trial slopes downhill to the west. Soil depths, moisture, and nutrients may increase along this slope improving site quality for greater HT growth in trial 2 (upper slope) compared to trial 1 (ridge top). The two trials did not differ significantly in DBH or VOL in any of the measurement periods from 1991 to 2009, suggesting that the differences in HT were largely driven by the environmental gradient. However, mean VOL of SEGI stecklings was greater in trial 2 at 109% of the overall steckling mean after 29 growing seasons.

It is important to note that while SEGI in trial 2 were interplanted with mixed conifer neighbors until thinning in 1999, the stecklings in trial 1 were interplanted with the much larger SEGI seedlings until thinning in 1999. Reconstructing the stand density (e.g., SDI) in the trials prior to thinning in 1999 would help establish the influence of

these competing trees on growth differences in SEGI stecklings in the two trials. This was not possible with the available data. Observation of the thinnings suggested that more large trees were removed from trial 1 than trial 2 (W.J. Libby, pers. comm.), with the effect that trial 1 trees likely had more available growing space following thinning. If this was the case and trial 2 had a higher stand density than trial 1, then the greater mean tree size in trial 2 may be understated by these results. As of 2009, SDI and basal area in trial 2 was ~50% greater than in trial 1. However, SDI of both trials accounted for the entire trial and not just the portion of the respective trials occupied by the stecklings.

It is possible that in the mixed species environment of trial 2, SEGI stecklings were better able to exploit resource niches not occupied by the other conifer species due to differences in timing of growth or belowground competition. In the pure SEGI planting in trial 1 it may be that all SEGI neighbors were competing for similar soil resources at near the same time thus limiting growth of individuals.

4.2 Performance of SEGI Grove Samples Related to Native Grove Area and Isolation

At FSO, native grove area (ha) and grove isolation by mean distance among sampled groves in latitude (°) were better predictors of SEGI HT than latitude or elevation of native-grove origin. While there were strong regional differences in growth of SEGI at FSO with trees from the central and south region of the native range performing better than trees from north region, the results of this analysis suggested that this may have more to do with the larger total area and the more continuous distribution of native groves within these regions than the latitude of the native grove.

In the north region, the eight SEGI native groves were smaller and more isolated than the larger and more continuously distributed groves in the central and south regions. Mean distance among grove samples from the north region was over twice as great (0.27° Lat) as those in the south region (0.10°) and over four times as great as grove samples in the central region (0.06°). Differences in mean grove area among regions were even more varied with mean grove area of ~89 ha for the north region groves, ~606 ha for the central region groves, and 843 ha for the south region grove samples. These geographic characteristics of native grove origin all contribute important information to understanding the population variation observed at FSO.

In my study, native SEGI grove area should be considered a proxy for population size with the assumption that the larger area native groves likely contain more abundant and more continuous distributions of SEGI individuals. The population size of a species is expected to positively correlate with both fitness and genetic diversity (Leimu et al. 2006). As indicated, SEGI population size by grove area correlates strongly with fitness by tree height at FSO. This suggested that the larger tree size of the grove samples from larger area native grove origins was related to the greater genetic diversity of these native groves. The hypothesized correlation between population size and genetic diversity was not well supported by the quantitative genetic information from the SEGI common-garden study at FSO. Genetic variances of SEGI stecklings grouped by small to large grove area categories showed no trend of increasing or decreasing genetic variance with grove area. This was also the case for the earlier isozyme analysis of the FSO SEGI seed collection for which there was no trend in SEGI genetic diversity by heterozygosity of

grove samples related to grove area categories (Fins and Libby 1982). However, strong correlations were found between SEGI native grove area and genetic diversity in recent microsatellite marker analysis of SEGI populations from the same rangewide seed collection from which the FSO SEGI trials were planted (Dodd and DeSilva 2016). In this analysis, SEGI genetic diversity at 11 microsatellite loci was greater in trees of larger area native grove origin (Dodd and DeSilva 2016). These results provide evidence that the greater mean tree size of grove samples originating from larger area native groves at FSO may be a result of their greater genetic diversity.

Further research into the importance of SEGI grove area as a predictor of tree size should focus on the demographics of native SEGI groves. Provided reliable grove inventory data of mature SEGI within native groves, it would be interesting to see if the number of mature trees within groves would be a stronger predictor of tree size than-grove area at FSO.

4.2.1 Influence of harvest history and elevation on HT in large SEGI grove samples

Among a subset of the SEGI steckling grove samples originating from the large and very-large native groves planted at FSO, elevation of native grove and harvest history of native grove were the best predictors of SEGI tree HT after 29 growing seasons. By controlling for the strong effect of grove area in the rangewide grove samples at FSO, trends in the effect of native grove elevation and harvest history on SEGI HT were observed in these grove samples from the central and south region of SEGI's range. Grove samples from lower elevations at FSO tended to be taller among just these large

and very large grove samples at FSO. Grove samples that had a history of timber harvesting had greater HT at FSO.

In this sub-sample, the grove sample from the highest elevation native grove Atwell Mill had the lowest mean HT at age 29. A moderate negative correlation between SEGI height and elevation of origin was observed in seedlings in year two (Guinon 1982). In other Sierra Nevada conifers, including PIPO, PILA, and ABCO elevation of seed origin was strongly related to HT growth in common-garden trials with trees from the highest elevation sites performing more poorly (Conkle 1973, Hamrick 1976, Kitzmiller 2004). These Sierra conifers were drawn from populations with greater variation in source elevation than the SEGI grove samples. The PILA samples varied in source elevation by >2000 m (Kitzmiller 2004) and ABCO within a local region may vary in source elevation by ~700 m (Hamrick and Libby 1972). Within this SEGI large-grove sub-sample, the variation in lowest to highest elevation native grove was ~350 m. The highest elevation Atwell Mill was 100 m higher than the next highest elevation native grove. When adjusted for latitude, the total variation of SEGI native grove elevation was just 485 m at FSO. The small elevation effect on HT in the rangewide FSO data could be attributed to this limited elevational range of SEGI grove samples. The raw elevations varied by only 735 m, from 1400 m for North Calaveras to 2135 m for Atwell Mill. The entire native range of the species occurs at so-called “montane elevations” in the Sierra Nevada with relatively similar environmental conditions.

There were no grove samples from the north region in this subset. All grove samples originated in native groves from the central and south region. It is important to

note that among these grove samples with large area, latitude of native grove was positively correlated with SEGI tree HT. This was evidence for the better performance of trees from the more northern portion of these more southern native SEGI groves. In the rangewide SEGI samples latitude was negatively correlated with tree height. This was evidence against a strong clinal trend in SEGI tree height from north to south in the grove samples at FSO.

Several of the best performing SEGI grove samples have documented histories of harvesting and other management activities within the native groves. The top performing grove sample at FSO, Mountain Home, has been managed as part of the Mountain Home State Forest since 1946. Harvesting of large SEGI occurred in the early 20^{th} C. and pine became the focus of partial harvests until acquisition by the state in 1946. From 1897-1905, harvesting of Converse Basin grove generated ~900,000 m^3 of SEGI logs (Willard 2000). Post-harvesting fires occurred and some areas of the grove, like Stump Meadow, were converted from SEGI mixed conifer forest to meadows (Willard 2000). At this time large SEGI were given protected status in the Mountain Home State Forest.

Past harvesting activities within the native groves may have influenced mating patterns by opening the stands and possibly increasing pollen flow among more distant trees in groves. Establishment and recruitment of new SEGI cohorts requires relatively severe disturbances and large canopy gaps (Stephenson 1994, York et al. 2009). Within SEGI native groves, SEGI comprises only about 5% of the stems and these are often widely spaced and interspersed with white fir and sugar pine (Rundel 1972). Harvesting events may have created canopy gaps that allowed for greater pollen flow between more

distant SEGI neighbors. This greater pollen flow may have increased outcrossing within these harvested groves and led to establishment of new cohorts better adapted to the 20th C. climate. Seed collected from these more recently established individuals may have performed better at FSO

The canopy gaps created by these disturbances may have led to regeneration events occurring in the early 20th C. which resulted in establishment of outcrossed SEGI better adapted to a 20th C. climate and thus better performing propagules at FSO. Further investigation of mating patterns within SEGI native groves and the influence of spacing between SEGI neighbors on pollen flow will help elucidate the relationship between disturbance, gene flow, and propagule performance. Research linking the size of canopy gaps necessary for SEGI regeneration events with amounts of outcrossing promoted by varying gap sizes would provide valuable information for the conservation of SEGI genetic diversity.

4.3 Differences in SEGI Steckling and Seedling Tree Size and Form Traits after 29 Growing Seasons

One of the questions the FSO SEGI trials were established to answer was whether SEGI stecklings would grow at similar rates to SEGI seedlings when outplanted. After 29 growing seasons at FSO, SEGI stecklings were significantly smaller than SEGI seedlings in HT, DBH, and VOL with lower height-diameter ratios. Part of these differences can be attributed to a nursery effect that caused many SEGI stecklings to check their growth in the first few years following planting. The seedlings were non-significantly larger than

SEGI stecklings after one year's growth as of 1981. From 1981-1983, the SEGI seedlings grew faster than the stecklings in HT, with highly statistically significant differences in mean relative height growth rate (RGRht), leading to statistically significant differences in mean HT83 in year 3 (1983). This early difference in mean tree HT83 was maintained through HT09 and resulted in a large and statistically significant difference in mean tree volume between SEGI stecklings and seedlings at age 29.

The stecklings and seedlings differed in relative growth rates only in the periods 1981-83 (earliest period data was available) and 1991-1997. In all other years relative height growth differences were non-significant. The significant difference in growth rate following thinning in 1991 was likely due to the larger seedlings with their larger crowns being better able to respond to the increase in growing space availability. At this time, stecklings were still growing intermixed with the seedlings and it may be that larger neighboring seedlings outcompeted the stecklings for the additional growing space. Following the thinning in 1999 that separated SEGI stecklings from seedlings, the mean RGRht of stecklings did not differ significantly from seedlings. The smaller steckling trees would be expected to have faster growth rates than larger seedling trees at this time, so this may be evidence for the better growth of seedlings than stecklings at FSO. However, the steckling diameter (RGRd) and volume (RGRv) relative growth rates were statistically significantly greater than that of seedlings. The smaller stecklings were increasing in DBH and VOL faster than the seedlings once they were no longer competing directly.

The large differences in size between the stecklings and the seedlings at age 29 may have been largely the product of the nursery effect and the resulting large early size differences which continued to compound as the larger neighbor seedlings outcompeted the smaller stecklings, until they were separated in 1999 by thinning. A strong conclusion as to whether SEGI stecklings will lag behind seedlings in outplantings was largely confounded by the nursery effect at FSO. Outplanting of SEGI stecklings may result in reduced height or volume growth compared to seedlings.

4.3.1 Stem form traits

A potential benefit of clonal forestry and the planting of vegetatively propagated stecklings has been the unconfirmed observation that stecklings may exhibit lower levels of undesirable stem form traits like basal swelling which will lead to inefficient utilization of stemwood volume at the mill. At FSO after 29 growing seasons, the stecklings and seedlings were expressing similar levels of basal swelling (SWEL). However, there were large differences in mean tree size of stecklings and seedlings which the visual assessment of SWEL may not have accounted for. This differed from the trend that was observed in *Sequoia sempervirens* (SESE), in which SESE stecklings consistently expressed less basal swelling than seedlings (Rydelius and Libby 1993). At FSO, there was no support for the observation that stecklings may produce less basal swelling than seedlings.

The other form traits assessed at FSO were expressed by the SEGI planting stock consistently with the trends in these traits as related to tree size at FSO. The smaller SEGI stecklings produced statistically significantly more epicormic sprouts (EPI) than

seedlings, which was the trend for smaller trees at FSO. The larger seedlings expressed more fluting (FLUT) of the lower stem, while both planting stock types expressed comparable amounts of lower stem asymmetry. The stecklings also expressed greater levels of crown fullness (FULL), which could indicate a tendency in the stecklings to allocate more resources to branch growth than stem growth. The stecklings also had statistically significantly lower mean HDR than seedlings at age 29. At this age HDR was moderately positively correlated with VOL ($r_s = 0.32$) suggesting stecklings may be stockier trees with less mean VOL than seedlings.

The findings at FSO were inconclusive as to whether SEGI stecklings or seedlings express better form traits from a timber perspective. Both types of planting stock exhibited form problems that may result in less efficient timber utilization.

4.4 Competitive Effects of Mixed Conifer Species and Brush Competition on SEGI Growth

The expectation that the SEGI seedlings would outgrow the five mixed conifer species in the mixed planting in trial 2 was not met after 29 growing seasons at FSO. *Pinus ponderosa* (PIPO) had the largest mean HT09 and DBH09 in the planting by a wide margin followed by PILA. The mean HT09 of SEGI trees also trailed PSME, but SEGI mean DBH09 was greater than PSME. Both ABCO and CADE lagged behind in HT09 and DBH09.

Typically it has only been at the highest stand densities that SEGI has been outgrown by PIPO in field experiments (Stohlgren 1993, Peracca and O'Hara 2008,

Kitzmiller and Lunak 2012). A survey of mixed plantings north of SEGI's current native range indicated that SEGI was outgrown by PIPO on only 5% of plantations (Kitzmiller and Lunak 2012). In plantings of SEGI, PIPO, and PSME at age 20 in the Nelder plot at U.C. Berkeley's Blodgett Forest Research Station (BFRS, ~38.8° N), just south of FSO, PIPO had the largest mean diameter at all tree spacings. Mean height of SEGI was comparable to PIPO only at the widest spacings (Peracca and O'Hara 2008). In this same planting at BFRS, SEGI diameter was greater than PSME, while PSME height was greater than SEGI at the narrowest spacing; indicating SEGI's sensitivity to crowding.

At FSO, SEGI and CADE were the tallest and largest trees in the mixed planting after 6 growing seasons in 1986. It was during the driest years at FSO from 1986 to 1991, that PIPO overtook SEGI for the largest mean height and diameter. Mean periodic annual precipitation for these years was significantly lower than during the other measurement periods at FSO (Figure 51), and below the long term mean by ~200 mm annually. The more drought adapted Pinaceae species, particularly PIPO, performed well during this period while both Cupressaceae species, SEGI and CADE, grew more poorly. In plantings outside of SEGI's native range, PIPO will likely be a strong competitor with SEGI. Ponderosa pine is a fast-growing shade intolerant pioneer species and will likely compete for a similar niche as SEGI in mixed plantings. In native SEGI groves, SEGI dominates in terms of basal area and was found in areas with greater soil moisture, while PIPO tended to be a minor species in basal area and was found on drier grove margins (Rundel 1971). With forecasts for increased drought stress in the Sierra Nevada (Hayhoe et al. 2004, van Mantgem et al. 2009), SEGI groves are likely to become drier leading to

a reduced number of sufficiently moist microsites for SEGI leading to a potential increase in PIPO abundance within SEGI groves.

The native SEGI groves tended to be dominated by ABCO and PILA in terms of density and relative canopy cover with CADE commonly found in the understory of native groves at lower elevations (Rundel 1971). At FSO, ABCO mean HT and DBH were well below the overall mixed conifer mean, while PILA had greater mean HT and DBH than SEGI. In the most recent measurement period from 1997 to 2009, both PILA and ABCO had the largest mean relative HT and DBH growth rates.

In models of neighbor competition indices (NCI), ABCO competition was a highly significant predictor of SEGI diameter increment with a large negative coefficient. This was evidence that ABCO was a strong competitor of SEGI at FSO from 1997 to 2009 despite its below average size. The large mean RGRh09 of ABCO indicated that as the trial became more crowded, this shade tolerant species was able to maintain growth relative to the other species (Figure 53) exploiting the more limited resources of the site.

In the absence of fire and anthropogenic disturbance in native SEGI groves, ABCO has been increasing in abundance throughout the 20th century (Bonnicksen and Stone 1982, Piirto and Rogers 2002). The FSO data suggested that ABCO may be a strong competitor to SEGI in the native groves and in plantings outside of the native range. In a SEGI common-garden study in Idaho, the observation was made that SEGI growth began each growing season approximately one month later than reported for local species (Du and Fins 1989). It has been noted that SEGI may begin growing later than local species. In a study of growing season timing and cessation in Sierra Nevada mixed

conifers, ABCO began HT and radial growth later in the season than the other mixed conifer species (Fowells 1941). It may be that ABCO was a strong competitor with SEGI due to similarity in the timing of their growing seasons leading to competition for the same limited resources.

In contrast to ABCO, PILA had one of the lowest coefficients in NCI models indicating that PILA had little discernible effect on SEGI diameter growth. The NCI model of SEGI diameter increment improved by AIC_c when PILA competitors were removed. This suggested that PILA was not a strong competitor of SEGI at FSO despite its larger mean size and rapid growth rate during the 1997 to 2009 period. Reports of the timing and duration of PILA growth indicated that this species ceased HT growth earlier than other Sierra conifers and had a shorter duration of radial growth, ceasing earlier than ABCO (Fowells 1941). The timing of SEGI and PILA growth may differ such that there was less direct competition for resources between the two species at FSO. It has previously been observed that planted SEGI tends to do well where PILA grows well (W.J. Libby, pers. comm.).

When planting SEGI with mixed conifer species, choosing sites with adequate soil moisture availability (Ray 2016) and maintaining wide spacings (Stohlgren 1993, Peracca and O’Hara 2008, Kitzmiller and Lunak 2012) will provide a competitive advantage to SEGI. Additionally, limiting the number of ABCO and PIPO near neighbors in favor of PILA, and possibly PSME, may further reduce the impact of competition on SEGI growth.

4.4.1 Effects of brush competition on SEGI and mixed conifer growth

The interaction of SEGI with brush species and the physiology of SEGI mycorrhizae are largely unknown. Like other members of Cupressaceae, SEGI is endomycorrhizal, associating with arbuscular mycorrhizal (AM) fungi (Kough et al. 1985). Seedlings that have been inoculated with AM were larger than non-inoculated SEGI seedlings (Kough et al. 1985) and generally had greater productivity and health (Molina 1994).

Observations at BFRS suggested that SEGI would perform better than PIPO when planted with *Ceanothus* and PIPO would perform better when both were planted with *Arctostaphylos* (Heald and Barrett 1999, W.J. Libby, pers. comm.). This was not the case in trial 3 at FSO where PIPO outgrew SEGI by a wide margin across *Arctostaphylos*, *Ceanothus*, and bare ground planted without brush species treatments. The nitrogen-fixing *Ceanothus* species, which also associate with AM (Rose 1980) were expected to improve the site for SEGI, either through the release of nitrogen or the facilitation of AM colonization that aid in growth. In trial 3 at FSO, SEGI mean volume in blocks planted with *Ceanothus* approximately equaled mean volume in blocks planted with *Arctostaphylos*, while SEGI volume was greatest planted in bare ground without brush species. There was no indication of a beneficial interaction with *Ceanothus* species in trial 3 at FSO. The presence of PIPO in the *Ceanothus* plots with SEGI may have contributed to this result. In laboratory and field studies, AM inoculum was absent in the understory associated with live PIPO trees (Kovacic et al. 1984). It may be that the presence of PIPO inhibited AM colonization of SEGI roots, thus negating any benefit

from the presence of *Ceanothus*. However, in greenhouse experiments, direct inhibition of AM colonization by PIPO was not observed (Kovacic et al. 1984).

Trial 3 was the highest density planting at FSO with trees planted at close spacing (1.5 m × 3.0 m) for a planting density of 2200 stems per hectare. *Sequoiadendron giganteum* volume has been shown to be more sensitive to high stand density than PIPO (Heald and Barrett 1999, Peracca and O'Hara 2008, York et al. 2013b) and this may have contributed more to the poor performance of SEGI in trial 3 than the brush competition.

In trial 3 at FSO, stemwood volume was greatest on bare ground planted without brush species for all conifers, except PSME, which had greatest volume in *Arctostaphylos* blocks. Both PSME and *Arctostaphylos* form ectomycorrhizal (EM) fungal associations and there has been evidence that *Arctostaphylos* presence promotes EM colonization of PSME in nursery soils (Hagerman and Durall 2003). Ectomycorhizal colonization may enhance the ability of PSME seedlings to withstand summer drought by increasing uptake of soil moisture thus maintaining high photosynthetic rates (Dunne and Parker 1999). In field studies, productivity and survival of PSME increased when planted with *Arctostaphylos* species (Howard 1992, Horton et al. 1999).

The performance of the conifers on bare ground would seem to confirm the value of brush control for productive volume growth. Further research into the effects of brush treatments on SEGI growth should be conducted with greater replication of treatment blocks. Including a treatment block in which SEGI is planted with the brush species and both with and without PIPO will test whether PIPO has an effect on SEGI growth in the *Ceanothus* plots.

4.5 Heartwood Decay Resistance of SEGI Thinned Stumps

The analyses of heartwood decay resistance were largely inconclusive, with results in the two seedling and standard clone thinned stump samples in disagreement. There was significant variation in standard clone stump heartwood decay resistance among regions, but no such trend in the seedling stumps (Table 29, Figure 53).

There were no significant differences among grove samples for seedling or standard clone data with the overall mean of ~2, on the high side of the scale. This may be an indication that most stumps were still reasonably free of decay 11 years after thinning. It may be that sufficient time had not passed in 2009 for pronounced differences in decay to have been expressed. If this was the case, the assessment could be repeated > 15 years after thinning. In both planting stock types, the correlation between decay resistance and DBH97, the diameter of trees two years before thinning, was weak ($r_s \leq 0.16$). This suggested that the differences in decay resistance that were assessed were not strongly related to size of the thinned stump.

4.6 Limitations and Recommendations for Future Research

The greatest limitation of this study of SEGI population variation was the lack of clonal replication across the two trials. If there had been two surviving ramets in both trial 1 and 2 of clones from a greater number of the sampled groves, variance components could have been estimated for among-grove and within-grove variance. This would have allowed for the calculation of an estimate of rangewide genetic variation both among-

groves and within groves across the two trials, which would better quantify SEGI genetic architecture. My thesis offers only a first glimpse of rangewide genetic variation in SEGI after 29 growing seasons.

Further study of SEGI genetic architecture would benefit from a clonal study replicated at multiple sites in order to assess genetic variation and heritability across a range of environmental site conditions. Seed collection and outplanting for this or other objectives should focus on a smaller number of groves within each region with greater replication of clones within groves to better assess this important component of genetic architecture. I would recommend an approach that analyzes geographically adjacent paired native grove samples from within each region. The paired grove samples should minimize differences in latitude of grove origin while maximizing differences in grove area. If possible, selecting seed from high elevation and low elevation sites within each grove would further the understanding of within grove variability along an elevational gradient. Paired native groves that offer the desired contrasts would be: North Calaveras and South Calaveras groves in the north region; Cabin Creek and Converse Basin in the central region; and Cedar Flat/South Fork and Garfield in the south region. Alternatively, native groves at similar latitudes, but varying east and west longitudes may be informational, with two good candidates being Black Mountain Grove and Freeman Creek Grove, the most eastern native SEGI grove.

Investigation of genetic architecture should also focus on the native groves in marginal habitats in terms of latitude and elevation. The high elevation Atwell Mill Grove would be a good candidate for future study. The Packsaddle Grove, the

southernmost non-Deer Creek grove also bears further investigation as it had one of the highest relative growth rates in the most recent period of growth at FSO from 1997 to 2009. Large native groves that were not sampled by the steckling genetic variation study like Garfield Grove may be good sources for outplanting and study. Garfield seedling grove samples were one of the top performing seedling grove samples planted at FSO.

The observed differences in HT09 growth between SEGI stecklings in trial 1 and trial 2 at FSO could be better understood by investigating microsite differences between the two trials. An analysis of soil water holding capacity and nutrient availability within these trials would help to explain whether the differences in HT growth are microsite related or may be due to competitive differences in SEGI growth in pure and mixed plantings. These measurements should be done both early in the growing season and late in the growing season when the Pinaceae species have ceased growth, but SEGI and CADE may still be growing depending on resource availability. These soil data will also help to determine habitat differences between the FSO study site and groves in the native range. This will also help to better understand the relatively poor growth of SEGI in comparison to PIPO, PILA, and PSME at FSO after 29 growing seasons.

The analysis of brush competition had limited power because only two replicates of each treatment were installed and the close spacing may have confounded the performance of SEGI in the brush plantings. Future sites should be planted at wider spacing (3.0 m × 3.0 m) and with greater replication of treatment blocks. I recommend an additional treatment of blocks planted with brush species and with and without PIPO to test whether PIPO has an effect on SEGI growth in the *Ceanothus* plots.

The decay status of cut stumps was difficult to assess because the criteria of decay in stumps was not well established by my measurements. Many stumps had sound heartwood at the time of measurement in 2010 and my assessment may not have captured the variability present in this trait. A better understanding of the signs of decay in SEGI heartwood, such as cracks, crumbling, and animal damage will be necessary to establish the appropriate categories of decay. It may be that decay in stumps had not proceeded to a degree that variability among stumps was evident at the time of measurement in 2009. The assessment should be repeated in 5 to 10 years from assessment in 2009 when decay in cut stumps should have progressed so that variation among stumps will be more evident.

I collected increment cores from a subset of 45 stecklings from four grove samples in July 2010. I cored all stecklings from two low elevation groves, South Calaveras (1365 m adjusted elevation, n = 13) and Grant (1210 m adjusted elevation, n = 10); and two high elevation native groves, Windy Gulch (1669 m adjusted elevation, n = 7) and Atwell Mill (1780 m adjusted elevation, n = 15) to capture the variability in this native grove geographic characteristic. This was done for the purpose of analyzing annual increment growth response to climatic variation over the 29 growing seasons at FSO and relate this to geographic characteristics of native grove origin. A more powerful genetic analysis could be done with increment cores taken from all two-ramet clones, but this was not done. I conducted none of this analysis. The next step would be to re-measure the increment cores and conduct the analysis. Increment cores collected at FSO present a

future researcher with a limited analysis of variation in climate-growth relationships among four grove samples.

I recommend caution when drawing inferences from Figures 51 and 52 where growth and climate appear linked because the impacts of climate on tree growth can be delayed for one or several years. Precipitation from the previous one or two years may have a stronger correlation with current year's growth than the current year precipitation (Dolanc et al. 2013).

4.7 Implications for SEGI Management and Conservation

Based on findings of the importance of grove area, grove isolation, and harvest history to tree size at FSO, the large groves in the central and south of SEGI's native range are recommended for future seed collections. Mountain Home, Converse Basin, Giant Forest, and Redwood Mountain are all recommended as seed sources for future outplantings based on their superior performance at FSO. Garfield grove, which did not have stecklings planted at FSO for analysis, should be a candidate for seed collection given the large grove area, history of harvesting within this grove, and high ranking of Garfield seedlings in the seedling grove sample study at FSO. South Calaveras was the best performing north region grove at FSO and is the largest of the north region native groves by area. This northern native grove would be a good option for seed collection in order to maintain genetic diversity in outplantings from throughout the native range.

Native grove area was the strongest predictor of SEGI tree size at FSO and there was evidence from microsatellite marker analysis that the larger area native groves are

more genetically diverse. Therefore, protecting and maintaining current extent and area of individual SEGI native groves will be a necessary objective of any conservation strategy for the species. The establishment of the Giant Sequoia National Monument (2000), encompassing all of the central and south region groves sampled at FSO that were not previously protected in Sequoia and Kings Canyon National Parks, would appear to have largely secured this objective. However, increasing stand density, increasing abundance of shade tolerant species such as white fir (ABCO) (Bonnicksen and Stone 1982, Piirto and Rogers 2002, Levine et al. 2016), and predictions for continued warming and drying within the native range (Hayhoe et al. 2007, van Mantgem et al. 2009) pose challenges to the resilience of current native grove habitat.

The strong performance of grove sample trees with origins in Mountain Home and Converse Basin native groves at FSO, groves in which partial harvesting has removed both SEGI and mixed conifers during the 19th and 20th Centuries, may demonstrate that these large native groves have been resilient to anthropogenic disturbance. These stands may have benefitted from these harvesting activities which created large gaps promoting SEGI regeneration and growth of residual SEGI trees (Peracca and O’Hara 2008, York et al. 2009, York et al. 2010, York et al. 2013b). Future studies should concentrate on establishing the correlation of population size, stand density, and species composition to genetic diversity within native groves in order to better understand how demographic shifts within native groves may alter SEGI genetic resources.

Table 1. Grove characteristics of 23 SEGI native grove samples planted at Foresthill Seed Orchard study site arranged from north to south in the table.

Grove name	Grove	Size Class	Area (ha)	Region	Lat (°)	Long (°)	Elev (m)	Adj Elev (m)
Foresthill Seed Orchard					39.08	120.73	1280	1284
Placer	11	Tiny	1	North	39.05	120.57	1585	1585
North Calaveras	12	Small	24	North	38.28	120.30	1400	1295
South Calaveras	13	Medium	184	North	38.25	120.23	1475	1365
Tuolumne	14	Small	8	North	37.77	119.80	1705	1529
Merced	81	Small	8	North	37.75	119.83	1675	1497
Mariposa	15	Medium	101	North	37.52	119.60	1890	1680
Nelder	16	Medium	195	North	37.45	119.58	1830	1611
McKinley	17	Small	22	North	37.02	119.10	1950	1671
Cabin Creek	21	Small	40	Central	36.80	118.95	1660	1352
Converse Basin	22	Very large	1498	Central	36.80	118.95	1755	1447
Lockwood	23	Small	40	Central	36.80	118.85	1675	1367
Windy Gulch	24	Large	405	Central	36.78	118.82	1980	1669
Grant	82	Medium	130	Central	36.75	118.98	1525	1210
Redwood Mountain	25	Very large	1271	Central	36.70	118.92	1905	1583
Giant Forest	26	Large	855	Central	36.56	118.75	1905	1564
Atwell Mill	31	Large	383	South	36.46	118.70	2135	1780
Cedar Flat/South Fork	83	Med	97	South	36.36	118.70	1948	1579
Mountain Home	32	Very large	1620	South	36.23	118.68	1890	1504
Wheel Meadow	35	Large	498	South	36.12	118.57	1950	1546
Black Mountain I	33	Large	1333	South	36.10	118.65	1945	1543
Black Mountain II	34	Large	1333	South	36.10	118.65	1950	1546
Packsaddle	36	Medium	137	South	35.93	118.58	1950	1523
Deer Creek	85	Tiny	21	South	35.92	118.58	1830	1401

Table 2. Climate summary of the Foresthill study site and a subset of six native SEGI groves of 23 sampled at Foresthill Seed Orchard arranged by latitude from north to south for the period 1981-2009. Climate data generated from Daymet database. Data are mean annual precipitation (Ann. Precip), mean monthly growing season (GS = May-Sept) precipitation, mean May snow water equivalent (SWE kg m^{-2}), mean monthly growing season temperature (Temp), and mean monthly growing season maximum (Max Temp) and minimum temperature (Min Temp).

Site	Ann. Precip (mm)	Growing Season Precip (mm)	May SWE (kg m^{-2})	GS Temp (°C)	GS Max Temp (°C)	GS Min Temp (°C)
Foresthill Seed Orchard	1300	147.3	0	18.3	25.3	8.9
North Calaveras	1355	106.3	2.8	16.3	23.5	4.4
South Calaveras	1363	107.8	1.6	15.8	23.0	8.7
Converse Basin	990	91.6	28.5	15.2	22.5	8.0
Giant Forest*	1110	79.7	274.2	12.8	20.0	5.5
Atwell Mill*	1167	77.3	523.8	10.6	17.8	3.5
Mountain Home	929	55.4	125.2	13.7	19.0	7.5
Packsaddle*	883	55.7	170.8	12.9	21.1	4.8

*Daymet data estimates a higher elevation site than SEGI native grove data. Mean precipitation and SWE may be overestimated, while temperature data may be underestimated.

Table 3. Distance dependent competition indices (CI) for nearest neighbor analysis of SEGI seedlings in mixed conifer planting of trial 2 at Foresthill Seed Orchard.

Competition Index	Equation
CIHegyi	$(DBH_j/DBH_i)/(D+1)$
CIDist	$(DBH_j/DBH_i)/D$
CI2Dist	$(DBH_j/DBH_i)/(D*2)$
$CIDist^2$	$(DBH_j/DBH_i)/D^2$
$CIDBH^2$	$(DBH_j/DBH_i)^2/D$

Where DBH_i is subject tree diameter, DBH_j is competitor tree diameter, and D is the distance from subject tree to competitor tree.

Table 4. Descriptive statistics summarized for trial 1 SEGI steckling by grove sample for height (m) (HT), diameter at breast height (cm) (DBH), conic stem volume (m^3) (VOL), and height-diameter ratio (HDR) in 2009 after 29 growing seasons at Foresthill Seed Orchard. Grove sample rankings (R) included (1 = largest; 23 = smallest).

		HT					DBH					VOL					HDR				
Grove	n	Mean	s.d.	Max	Min	R	Mean	s.d.	Max	Min	R	Mean	s.d.	Max	Min	R	Mean	s.d	Max	Min	R
Placer	8	6.2	2.1	9.9	3.6	22	14.8	3.9	20.2	9.4	23	0.04	0.03	0.11	0.01	23	42	4.2	49	38	2
North Calaveras	19	8.9	2.6	15.9	3.8	19	23.3	5.2	32.8	9.7	20	0.15	0.09	0.45	0.01	19	38	3.7	49	33	10
South Calaveras	13	10.1	2.4	13.6	6.4	11	28.4	5.7	38.2	21.1	4	0.24	0.14	0.47	0.07	5	35	4.1	43	30	16
Tuolumne	12	9.3	3.1	15.2	5.8	16	24.6	6.9	35.2	14.8	18	0.18	0.15	0.49	0.03	16	38	4.9	44	31	12
Merced	10	7.6	2.3	11.3	4.2	20	24.2	6.3	33.1	13.5	19	0.14	0.10	0.32	0.02	20	31	3.4	36	26	23
Mariposa	8	9.7	1.6	11.8	7.3	13	26.9	4.7	34.4	18.4	11	0.20	0.09	0.37	0.07	12	36	4.6	42	26	15
Nelder	6	9.0	1.8	10.5	6.3	18	25.3	4.0	31.2	20.2	16	0.16	0.07	0.27	0.07	18	35	3.7	40	31	16
McKinley	13	10.0	2.6	15.3	5.8	12	26.7	3.5	33.2	20.3	13	0.20	0.10	0.44	0.06	12	37	6.8	52	29	14
Cabin Creek	10	9.4	1.8	11.8	5.4	15	26.6	3.7	32.8	20.5	14	0.18	0.08	0.33	0.06	16	35	4.2	40	26	16
Converse Basin	14	11.7	1.8	15.5	9.3	2	29.0	4.1	37.4	23.7	2	0.27	0.12	0.57	0.14	3	41	3.5	46	34	3
Lockwood	11	10.4	2.9	14.4	6.8	9	26.7	6.3	36.2	18.3	12	0.22	0.14	0.48	0.06	10	39	4.8	48	32	6
Windy Gulch	5	10.3	1.7	12.8	8.4	10	27.1	4.4	34.0	22.2	10	0.21	0.11	0.39	0.11	11	38	2.9	41	34	8
Grant	7	9.2	2.6	14.2	6.6	17	28.8	6.5	38.9	18.3	3	0.23	0.17	0.56	0.06	7	32	4.9	39	26	21
Redwood Mtn	19	10.6	3.3	15.9	4.6	6	27.5	6.0	35.5	14.8	8	0.24	0.15	0.52	0.03	5	38	5.9	46	30	9
Giant Forest	11	11.1	3.1	16.3	6.3	3	28.4	8.0	39.1	16.0	5	0.28	0.21	0.65	0.04	2	39	4.0	45	33	5
Atwell Mill	10	9.6	3.2	15.0	4.1	14	24.7	7.8	37.0	10.9	17	0.19	0.16	0.47	0.01	14	39	4.8	45	32	7
Cedar Flat	3	7.2	3.2	10.6	4.4	21	22.2	6.9	28.0	14.6	21	0.11	0.10	0.22	0.02	21	32	5.5	38	27	22
Mountain Home	11	12.0	3.1	17.1	8.0	1	33.8	6.8	47.9	25.9	1	0.41	0.27	1.03	0.14	1	35	3.8	42	30	16
Wheel Meadow	13	10.6	3.1	15.3	5.6	6	27.9	5.9	37.0	16.5	6	0.25	0.14	0.48	0.04	4	38	6.0	51	28	13
Black Mountain I	13	10.8	2.8	16.7	7.6	4	27.4	4.9	36.7	20.9	9	0.23	0.15	0.59	0.09	7	40	7.2	51	28	4
Black Mountain II	8	10.7	2.1	12.8	7.4	5	25.3	4.0	30.3	20.4	15	0.19	0.09	0.31	0.09	14	42	3.5	47	35	1
Packsaddle	11	10.5	2.4	15.1	6.3	8	27.7	4.6	36.3	17.9	7	0.23	0.12	0.52	0.05	7	38	3.9	43	33	10
Deer Creek	2	6.2	3.4	8.6	3.8	22	18.9	10.3	26.1	11.6	22	0.08	0.10	0.15	0.01	22	33	0.1	33	33	20
All	237	9.9	2.8	17.1	3.6		26.5	6.3	47.9	9.4		0.21	0.15	1.03	0.01		37	5.3	52	26	

Table 5. Trial 1 SEGI steckling grove sample height (HT) in percent of within trial steckling mean by grove sample in six measurement years from 1981 to 2009 at Foresthill Seed Orchard. Coefficient of variation (CV) and grove sample rankings (R) included (1 = largest; 23 = smallest).

		1981			1983			1988			1991			1997			2009		
Grove	n	HT%	CV	R	HT%	CV	R	HT%	CV	R	HT%	CV	R	HT%	CV	R	HT%	CV	R
Placer	8	75	31	23	68	22	21	67	21	22	69	28	22	69	34	22	63	33	22
North Calaveras	19	95	25	14	102	34	10	100	31	16	103	31	12	98	32	13	90	29	19
South Calaveras	13	85	31	20	101	30	12	104	23	11	105	22	8	104	27	8	102	23	11
Tuolumne	12	105	30	12	85	28	19	88	30	19	92	23	18	96	25	15	94	33	16
Merced	10	110	21	7	80	30	20	75	34	20	77	30	20	76	32	20	77	30	20
Mariposa	8	95	39	13	89	36	18	88	40	18	95	30	17	94	23	17	98	17	13
Nelder	6	110	34	4	94	22	16	100	15	13	97	18	15	91	24	18	91	20	18
McKinley	13	90	28	18	110	17	4	108	18	6	105	17	8	102	25	9	101	26	12
Cabin Creek	10	110	20	5	94	21	15	100	26	15	97	23	15	89	24	19	95	19	15
Converse Basin	14	105	22	9	116	30	2	117	25	1	118	21	1	115	19	1	118	16	2
Lockwood	11	115	31	1	96	20	14	104	15	9	108	21	7	104	23	7	105	28	9
Windy Gulch	5	110	36	2	111	36	3	100	22	13	90	21	19	98	22	14	104	17	10
Grant	7	90	30	19	90	33	17	92	29	17	97	25	14	94	31	16	93	28	17
Redwood Mtn	19	110	26	6	107	37	6	108	39	7	108	32	5	107	36	5	107	31	7
Giant Forest	11	105	34	11	105	36	8	108	30	5	113	27	3	109	31	4	112	28	3
Atwell Mill	10	110	19	2	98	36	13	100	30	12	100	25	13	98	29	12	97	33	14
Cedar Flat	3	80	44	22	59	45	23	71	36	21	69	36	21	74	51	21	73	44	21
Mountain Home	11	85	30	21	107	27	7	113	22	3	113	25	2	115	27	2	121	26	1
Wheel Meadow	13	105	31	10	117	26	1	113	25	2	110	25	4	111	28	3	107	29	6
Black Mountain I	13	95	24	17	101	31	11	104	30	10	105	24	10	104	25	6	109	26	4
Black Mountain II	8	95	19	15	105	19	9	108	19	8	108	17	6	102	23	10	108	19	5
Packsaddle	11	105	27	8	109	31	5	113	20	3	103	16	11	100	17	11	106	23	8
Deer Creek	2	95	7	16	68	0	22	58	10	23	59	22	23	57	23	23	63	55	23
All	237		28			31			30			27			29			29	

Table 6. Trial 1 SEGI steckling grove sample stem diameter (DBH) and volume (VOL) in percent of within trial steckling mean by grove sample for three measurement periods from 1991 to 2009 at Foresthill Seed Orchard. Coefficient of variation (CV) and grove sample rankings (R) included (1 = largest; 23 = smallest).

		1991			1997			2009			1991			1997			2009		
Grove	n	DBH%	CV	R	DBH%	CV	R	DBH%	CV	R	VOL%	CV	R	VOL%	CV	R	VOL%	CV	R
Placer	8	50	35	21	58	43	22	56	27	23	16	87	22	25	88	22	19	82	23
North Calaveras	19	107	39	7	95	35	17	88	22	20	112	76	8	92	93	12	71	63	19
South Calaveras	13	105	40	8	108	29	5	107	20	4	110	84	9	117	81	6	114	58	6
Tuolumne	12	89	46	19	94	32	18	93	28	18	75	88	18	83	88	16	86	85	17
Merced	10	67	60	20	87	36	20	91	26	19	42	116	20	61	92	20	67	73	20
Mariposa	8	93	51	17	98	29	12	102	18	11	90	106	15	85	76	14	95	46	13
Nelder	6	102	37	10	95	29	15	96	16	16	90	73	16	79	75	18	76	47	18
McKinley	13	124	27	1	105	21	8	101	13	13	131	52	3	101	69	8	95	49	12
Cabin Creek	10	98	44	13	91	30	19	100	14	14	90	74	14	70	60	19	86	45	16
Converse Basin	14	117	26	3	113	18	2	109	14	2	135	67	2	129	52	3	129	44	3
Lockwood	11	103	21	9	103	22	9	101	24	12	92	60	12	99	62	9	105	65	10
Windy Gulch	5	92	36	18	96	29	13	102	16	10	69	69	19	83	66	15	100	51	11
Grant	7	96	49	15	108	37	4	109	23	3	93	88	11	115	89	7	110	72	9
Redwood Mtn	19	101	44	11	107	31	6	104	22	8	116	105	7	128	89	4	114	63	5
Giant Forest	11	107	41	6	109	38	3	107	28	5	128	88	4	139	95	2	133	74	2
Atwell Mill	10	97	52	14	96	38	13	93	32	17	101	107	10	96	89	11	90	83	15
Cedar Flat	3	45	63	22	70	47	21	84	31	21	17	132	21	43	122	21	52	89	21
Mountain Home	11	122	33	2	128	25	1	128	20	1	149	74	1	175	69	1	195	66	1
Wheel Meadow	13	108	34	5	107	27	7	105	21	6	119	84	5	119	68	5	119	58	4
Black Mountain I	13	96	38	16	101	22	10	103	18	9	92	99	13	96	77	10	110	65	7
Black Mountain II	8	113	36	4	95	16	15	96	16	15	116	64	6	80	52	17	90	47	14
Packsaddle	11	99	32	12	101	18	11	104	17	7	85	68	17	86	44	13	110	53	8
Deer Creek	2	32	64	23	49	47	23	71	54	22	6	111	23	14	98	23	38	124	22
All	237	100	41		100	31		100	24		100	88		100	83		100	71	

Table 7. Descriptive statistics summarized for trial 2 SEGI stecklings by grove sample for height (m) (HT), diameter at breast height (cm) (DBH), conic stem volume index (m^3) (VOL), and height-diameter ratio (HDR) in 2009 after 29 growing seasons at Foresthill Seed Orchard. Grove sample rankings (R) included (1 = largest; 21 = smallest).

		HT					DBH					VOL					HDR				
Grove	n	Mean	s.d.	Max	Min	R	Mean	s.d.	Max	Min	R	Mean	s.d.	Max	Min	R	Mean	s.d	Max	Min	R
Placer	5	6.3	1.9	8.9	4.2	20	14.3	4.1	19.2	8.5	20	0.04	0.03	0.07	0.01	20	45	5.8	52	39	10
North Calaveras	11	10	2.9	13.6	5.7	16	22.3	4.2	28.2	15.6	18	0.15	0.08	0.28	0.04	18	44	6.7	57	34	11
South Calaveras	9	11.1	3.5	15.8	5.2	14	27.0	3.5	30.8	19.4	7	0.22	0.10	0.33	0.07	11	41	11.3	58	20	16
Tuolumne	4	9.9	4.3	15.0	4.6	17	21.1	7.0	25.6	10.7	19	0.14	0.09	0.24	0.01	19	47	10.7	61	36	5
Merced	2	10.6	1.2	9.7	11.4	16	28.5	2.2	26.9	30.0	5	0.23	0.06	0.18	0.27	11	37	1.4	36	38	20
Mariposa	3	11.4	2.2	13.0	8.9	12	27.4	3.2	29.3	23.7	6	0.23	0.09	0.29	0.13	10	41	3.5	44	38	15
Nelder	5	9.9	3.1	13.0	5.1	17	25.2	7.1	31.3	14.9	14	0.20	0.13	0.33	0.03	15	39	3.4	43	34	19
McKinley	6	11.8	2.3	14.7	7.9	8	25.2	5.1	32.4	17.4	14	0.21	0.11	0.40	0.06	12	47	4.5	53	40	4
Cabin Creek	4	12.2	3.9	15.7	7.6	7	30.3	9.0	38.0	19.8	3	0.35	0.26	0.58	0.08	3	40	1.5	42	38	17
Converse Basin	10	13.9	4.2	19.9	7.6	2	30.7	10.7	55.1	16.8	2	0.44	0.44	1.58	0.06	2	46	6.5	56	34	7
Lockwood	7	12.3	3.8	16.9	8.1	6	25.7	7.3	38.6	17.3	12	0.25	0.21	0.62	0.06	7	48	11.1	66	35	2
Windy Gulch	5	13.1	1.9	14.8	10.6	4	27.0	3.6	31.3	22.6	7	0.26	0.10	0.37	0.14	6	49	5.7	58	43	1
Redwood Mtn	8	13.2	2.2	16.7	10.4	3	27.8	5.0	35.6	20.7	5	0.29	0.14	0.53	0.13	5	48	6.9	58	38	3
Giant Forest	3	12.8	3.7	16.6	9.3	5	29.6	5.8	35.1	23.5	4	0.32	0.20	0.54	0.13	4	43	4.1	47	40	14
Atwell Mill	9	11.8	3.1	15.6	4.9	8	26.2	7.3	36.1	10.0	11	0.25	0.15	0.53	0.01	9	45	4.0	53	40	8
Cedar Flat	5	9.9	2.3	13.4	7.2	17	26.5	3.6	32.3	22.9	9	0.19	0.10	0.37	0.10	17	37	4.2	42	31	20
Mountain Home	4	14.3	3.9	19.7	10.9	1	35.5	5.9	42.9	28.5	1	0.51	0.31	0.95	0.23	1	40	4.4	46	36	18
Wheel Meadow	10	10.7	3.8	15.3	5.5	15	24.5	6.5	33.8	15.2	17	0.20	0.15	0.44	0.03	13	43	7.1	57	31	13
Black Mountain I	6	11.5	2.8	13.8	6.7	11	24.7	5.1	32.9	16.9	16	0.20	0.10	0.33	0.05	14	47	9.5	58	36	5
Black Mountain II	4	11.6	4.0	17.3	8.1	10	26.5	6.7	35.9	20.1	9	0.25	0.22	0.58	0.10	8	43	7.4	49	33	12
Packsaddle	3	11.3	1.2	12.6	10.3	13	25.3	3.2	28.1	21.9	13	0.19	0.07	0.26	0.13	16	45	2.4	47	42	9
All	123	11.5	3.4	19.9	4.2		26.1	6.9	55.1	8.5		0.24	0.20	1.58	0.01		44	7.2	66	20	

Table 8. Trial 2 SEGI steckling grove sample height (HT) in percent of within trial steckling mean by grove sample in six measurement years from 1981 to 2009 at Foresthill Seed Orchard. Coefficient of variation (CV) and grove sample rankings (R) included (1 = largest; 21 = smallest).

		1981			1983			1988			1991			1997			2009		
Grove	n	HT%	CV	R	HT%	CV	R	HT%	CV	R	HT%	CV	R	HT%	CV	R	HT%	CV	R
Placer	5	68	22	21	63	42	21	63	35	21	62	29	21	56	31	21	55	30	21
North Calaveras	11	103	20	10	96	20	14	89	14	18	91	14	18	91	19	18	87	30	17
South Calaveras	9	107	22	8	88	40	18	94	27	15	97	24	14	98	29	13	97	32	14
Tuolumne	4	94	20	15	94	32	15	92	26	17	90	29	19	91	31	17	86	43	19
Merced	2	91	54	16	81	50	19	85	47	20	79	46	20	78	46	20	93	11	16
Mariposa	3	103	12	11	102	6	11	110	9	5	113	11	5	105	8	7	100	19	12
Nelder	5	91	19	16	105	28	8	101	30	12	94	26	17	90	30	19	87	31	18
McKinley	6	108	20	7	103	19	10	103	15	11	105	17	8	101	23	10	103	19	8
Cabin Creek	4	108	51	6	143	32	1	127	22	1	114	22	4	107	21	5	107	32	7
Converse Basin	10	104	33	9	105	32	9	109	22	6	116	23	3	123	31	2	121	30	2
Lockwood	7	89	34	18	78	38	20	86	29	19	95	23	15	100	26	11	107	31	6
Windy Gulch	5	117	34	2	116	38	3	107	35	7	103	23	10	102	19	8	115	15	4
Redwood Mtn	8	111	31	3	115	28	4	107	20	8	106	17	6	110	25	4	115	17	3
Giant Forest	3	110	8	4	109	43	6	123	35	2	119	32	2	114	37	3	111	31	5
Atwell Mill	9	102	41	12	89	21	17	94	18	16	98	19	12	99	26	12	103	32	9
Cedar Flat	5	86	29	20	91	16	16	98	18	14	94	14	16	95	24	15	86	16	19
Mountain Home	4	102	12	12	101	38	13	114	39	4	126	34	1	126	35	1	124	36	1
Wheel Meadow	10	95	49	14	112	28	5	103	23	10	97	24	13	96	28	14	93	33	15
Black Mountain I	6	86	24	19	102	28	11	100	22	13	103	16	9	105	19	6	100	25	11
Black Mountain II	4	118	64	1	105	30	7	106	25	9	105	31	7	101	40	9	101	35	10
Packsaddle	3	110	48	4	118	43	2	118	14	3	100	17	11	92	15	16	99	10	13
All	124		32			31			25			24			28			30	

Table 9. Trial 2 SEGI steckling grove sample stem diameter (DBH) and volume (VOL) in percent of within trial steckling mean by grove sample for three measurement periods from 1991 to 2009 at Foresthill Seed Orchard. Coefficient of variation (CV) and grove sample rankings (R) included (1 = largest; 21 = smallest).

		1991			1997			2009			1991			1997			2009		
Grove	n	DBH%	CV	R	DBH%	CV	R	DBH%	CV	R	VOL%	CV	R	VOL%	CV	R	VOL%	CV	R
Placer	5	45	51	21	48	42	21	55	29	21	14	100	21	15	79	21	16	73	21
North Calaveras	11	88	23	17	88	17	17	85	19	19	64	52	18	61	47	19	60	58	19
South Calaveras	9	101	37	11	105	33	7	103	13	9	100	81	10	110	76	8	90	43	12
Tuolumne	4	83	43	18	83	40	19	81	33	20	64	70	18	63	67	18	58	66	20
Merced	2	78	91	20	85	62	18	109	8	5	71	133	17	68	121	17	92	27	11
Mariposa	3	124	17	3	118	12	2	105	12	7	143	41	4	120	29	6	96	38	10
Nelder	5	91	48	16	99	32	11	97	28	16	86	82	13	88	78	13	80	65	16
McKinley	6	107	20	8	99	24	12	97	20	15	107	51	8	90	68	12	87	53	13
Cabin Creek	4	125	21	2	114	25	3	116	30	3	157	58	2	124	60	5	144	74	3
Converse Basin	10	113	33	5	113	33	6	118	35	2	143	67	4	161	83	2	180	99	2
Lockwood	7	79	45	19	92	32	16	98	28	13	64	115	18	85	84	14	102	82	7
Windy Gulch	5	109	34	6	102	23	9	104	13	8	121	72	6	95	54	10	106	37	6
Redwood Mtn	8	109	23	7	113	21	5	107	18	6	107	50	8	129	74	4	116	48	5
Giant Forest	3	119	27	4	113	30	4	113	20	4	150	66	3	139	69	3	131	63	4
Atwell Mill	9	99	33	12	101	33	10	100	28	12	93	55	12	100	76	9	101	60	9
Cedar Flat	5	99	30	13	95	28	15	101	14	11	86	70	13	83	79	15	79	53	18
Mountain Home	4	142	29	1	143	19	1	136	17	1	243	82	1	229	65	1	209	61	1
Wheel Meadow	10	101	33	10	99	31	12	94	27	18	100	71	10	93	70	11	83	74	14
Black Mountain I	6	95	17	15	97	16	14	95	21	17	79	48	15	83	37	15	81	48	15
Black Mountain II	4	106	38	9	104	35	8	102	25	10	121	88	6	112	99	7	102	90	7
Packsaddle	3	96	18	14	82	8	20	97	12	14	79	51	15	51	32	20	80	34	17
All	124		34			31			26			80			82			82	

Table 10. Variance components of tree size and form traits for trial 1 (n = 50) and trial 2 (n = 17) SEGI clone subset in six measurement years over 29 growing seasons at Foresthill Seed Orchard from 1981 to 2009. Significance codes for Pr>F: p < 0.1 (.), <0.05 (*), <0.01(**), <0.001(***), <0.0001(****).

	Among-Region Variance						Among-Clone Variance						Genetic Variance (%)	
Trait	Tr1 Est	Pr(F)	Tr2 Est	Pr(F)	Tr1%	Tr2%	Tr1 Est	Pr(F)	Tr2 Est	Pr(F)	Tr1 %	Tr2 %	Tr1	Tr2
HT81	0.0004	.	-0.0010		11	0	-0.0003		-0.0003		0	0	11	0
HT83	-0.0049		0.0073	.	0	10	0.0118		0.0179		17	26	17	36
HT88	-0.0272		0.0914	*	0	31	0.0352		0.0391		7	13	7	44
HT91	-0.0588		0.4277	*	0	39	0.2510	.	0.0807		23	7	23	46
HT97	-0.1338		0.7470	*	0	31	0.7769	**	0.1745		33	7	33	38
HT09	1.2489	**	5.8657	*	15	39	2.7915	**	1.1600		33	8	47	47
DBH91	-0.4829		1.8455		0	18	0.9175		-0.7315		5	0	5	18
DBH97	-0.9314		6.7889	*	0	39	3.9150		0.3450		18	2	18	41
DBH09	4.2717	*	25.4994	*	11	45	9.2700		-1.6950		24	0	35	45
VOL91	0.0000		0.0000	.	0	28	0.0000		0.0000		15	0	15	28
VOL97	-0.0001		0.0003	*	0	35	0.0004		-0.0001		32	0	32	35
VOL09	0.0044	**	0.0204	*	15	43	0.0080		-0.0068		27	0	42	43
HDR91	-8.1615		-8.7640		0	0	10.1950		-8.8250		6	0	6	0
HDR97	-1.1951		-3.7525		0	0	7.8085	**	6.3265		38	31	38	31
HDR09	-0.6696	**	-9.4392		0	0	21.9800	***	25.1950	*	80	52	80	52
FLUT	-0.0367		0.0440		0	5	-0.0836		-0.0736		0	0	0	5
ASYM	-0.0259		0.4256	*	0	37	0.0871		0.0357		11	3	11	41
SWEL	-0.0277		0.0931		0	17	0.1510	**	0.0405		34	7	34	24
FULL	-0.0512		0.2877	*	0	31	0.3681	***	0.1757		47	19	47	50
EPI	-0.0014		0.0112		0	16	0.0832	.	-0.0056		20	0	20	16

Table 11. Variance components of tree size and form traits for trial 1 and 2 combined SEGI stecklings assessing variation among-trials (Trial), among-regions (Region), among-groves (Grove), and the interaction of trial and grove (Tr*Grv) in six measurement years over 29 growing seasons at Foresthill Seed Orchard from 1981 - 2009. Heritabilities (H^2) are unitless. Significance codes for Pr>F: p < 0.1 (.), <0.05 (*), <0.01(**), <0.001(***), <0.0001(****).

	Trial			Region			Grove			Tr*Grv			Residual		H^2
Trait	Est	Pr(F)	%	Est	Pr(F)	%	Est	Pr(F)	%	Est	Pr(F)	%	Est	%	
HT81	0.002		38	0.000		8	0.000		0	0.000		0	0.003	57	0.08
HT83	0.002		3	-0.001		0	0.004		5	-0.006		0	0.069	92	0.05
HT88	1.694	***	75	0.127	.	6	0.008		0	-0.036		0	0.433	19	0.06
HT91	2.159	**	62	0.224	.	6	0.091		3	-0.095		0	1.036	30	0.09
HT97	3.187	*	49	0.546	.	8	0.310		5	-0.311		0	2.482	38	0.13
HT09	34.257	****	70	4.816	**	10	1.479		3	-1.157		0	8.460	17	0.13
DBH91	0.477		3	-1.792		0	0.791		5	-0.939		0	15.011	92	0.05
DBH97	-3.954		0	-2.075		0	4.369	.	18	-2.305		0	19.803	82	0.18
DBH09	-33.397		0	2.253	.	4	14.536	**	28	-4.826		0	35.170	68	0.32
VOL91	0.250		17	-0.117		0	0.025		2	-0.039		0	1.238	82	0.02
VOL97	-0.230		0	-0.003		0	0.132		13	-0.106		0	0.902	87	0.13
VOL09	-0.329		0	0.137	*	16	0.154	*	18	-0.081		0	0.554	66	0.34
HDR91	120.967	*	48	1.800		1	-8.527		0	10.060		4	116.800	47	0.00
HDR97	303.633	****	89	-5.271		0	5.123		1	-1.215		0	33.800	10	0.01
HDR09	797.133	****	94	8.814	*	1	8.620	*	1	-2.730		0	34.900	4	0.01
FLUT	-0.074		0	-0.028		0	0.073		9	-0.078		0	0.773	91	0.09
ASYM	0.435		31	-0.062		0	-0.102		0	0.071		5	0.916	69	0.00
SWEL	1.510	***	76	-0.119		0	0.108	**	5	-0.014		0	0.379	19	0.05
FULL	5.053	****	83	-0.206		0	0.222	**	4	-0.047		0	0.824	14	0.04
EPI	0.506	**	53	0.055	.	6	0.063	*	7	-0.011		0	0.335	35	0.12

Table 12. Descriptive statistics summarized for trial 1 and trial 2 SEGI steckling tree size traits by region of native grove origin after 29 growing seasons at Foresthill Seed Orchard in 2009 for height (HT09), stem diameter at breat height (DBH09), conic stem volume (VOL09), and height-diameter ratio (HDR09). Placer grove samples were not included in summaries. Significant differences indicated by letter groups (α = 0.05)

		Trial 1				Trial 2			
	Region	North	Central	South	All	North	Central	South	All
Trait	n	81	77	69	227	43	37	41	121
HT09 (m)	Mean	9.2[b]	10.5[a]	10.6[a]	10.1	10.6[e]	13.1[d]	11.4[e]	11.7
	s.d.	2.5	2.7	2.9	2.8	2.9	3.2	3.2	3.3
	Min	3.8	4.6	4.1	3.8	4.6	7.6	4.9	4.6
	Max	15.9	16.3	17.1	17.1	15.8	19.9	19.7	19.9
	% mean	91.1	104.0	105.0		90.9	112.0	97.7	
DBH09 (cm)	Mean	25.5[b]	27.8[a]	27.7[a]	26.9	24.7[e]	28.7[d]	26.5[e]	26.6
	s.d.	5.5	5.6	6.4	5.9	5.0	7.5	6.4	6.5
	Min	9.7	14.8	10.9	9.7	10.7	16.8	10.0	10.0
	Max	38.2	39.1	47.9	47.9	32.4	55.1	42.9	55.1
	% mean	94.6	103.1	102.9		92.9	108.0	99.5	
VOL09 (m^3)	Mean	0.18	0.24	0.25	0.22	0.19	0.33	0.25	0.25
	s.d.	0.11	0.14	0.17	0.15	0.10	0.27	0.18	0.20
	Min	0.01	0.03	0.01	0.01	0.01	0.06	0.01	0.01
	Max	0.49	0.65	1.03	1.03	0.40	1.58	0.95	1.58
	% mean	81.8	109.1	113.6		76.0	132.0	100.0	
HDR09	Mean	36.1	37.9	38.0	37.3	43.0	46.0	43.0	44.0
	s.d.	4.9	5.1	5.5	5.2	7.7	7.4	6.5	7.3
	Min	26.1	25.6	27.2	25.6	20.0	34.0	31.0	20.0
	Max	51.9	48.0	51.4	51.9	61.0	66.0	58.0	66.0
	% mean	96.8	101.6	101.9		97.7	104.5	97.7	

Table 13. Descriptive statistics summarized for trial 1 SEGI steckling (n = 237) tree size traits after 29 growing seasons in pure SEGI planting grouped by native grove area categories: tiny, small, medium, large, and very large. Significant differences indicated by letter groups (α = 0.05). Tiny* groves (Placer and Deer Creek) were not included in tests of significance indicated in table below.

	Parameter	Tiny	Small	Med	Large	V. Lg.	All
Trait	n	10	75	48	60	44	237
HT09 (m)	Mean	6.2	9.3[a]	9.7[a]	10.6[ab]	11.3[b]	9.9
	s.d.	2.1	2.6	2.3	2.8	2.9	2.8
	Min	3.6	3.8	4.4	4.1	4.6	3.6
	Max	9.9	15.9	15.1	16.7	17.1	17.1
	% mean	62.6	93.9	98.0	107.1	114.1	
DBH09 (cm)	Mean	15.6	25.2[a]	27.3[ab]	27.0[ab]	29.5[b]	26.5
	s.d.	5.2	5.4	5.3	6.1	6.1	6.3
	Min	9.4	9.7	14.6	10.9	14.8	9.4
	Max	26.1	36.2	38.9	39.1	47.9	47.9
	% mean	58.8	94.9	102.9	101.8	111.4	
VOL09 (m^3)	Mean	0.05	0.18	0.21	0.23	0.29	0.21
	s.d.	0.05	0.11	0.12	0.15	0.19	0.15
	Min	0.01	0.01	0.02	0.01	0.03	0.01
	Max	0.15	0.49	0.56	0.65	1.03	1.03
	% mean	23.8	85.7	100.0	109.5	138.1	
HDR09	Mean	40.0	36.6[ab]	35.3[a]	39.2[b]	38.1	37.4
	s.d.	5.3	5.2	4.5	5.3	5.1	5.2
	Min	32.8	26.1	25.6	28.1	29.8	25.6
	Max	49.0	51.9	43.2	51.4	45.6	51.9
	% mean	107.0	97.9	94.4	104.8	101.9	

*When tiny groves were included in native grove area categorical analysis, tiny groves differed significantly from all other categories In HT09, DBH09, and VOL09. No differences were detected among the other grove size categories.

Table 14. Descriptive statistics summarized for trial 2 SEGI steckling (n=121) tree size traits after 29 growing seasons grouped by native grove size categories: tiny, small, medium, large, and very large. Significant differences indicated by letter groups (α = 0.05). Tiny* Placer Grove was not included in tests of significance indicated in table below

		Tiny	Small	Med	Large	V. Lg.	All
Trait	n	5	32	25	37	22	121
HT09 (m)	Mean	6.3	11.1[a]	10.8[a]	11.7[ac]	13.7[c]	11.5
	s.d.	1.9	3.2	2.7	3.2	3.4	3.4
	Min	4.2	4.6	5.1	4.9	7.6	4.2
	Max	8.9	16.9	15.8	17.3	19.9	19.9
	% mean	55.3	96.5	94.1	101.8	119.6	
DBH09 (cm)	Mean	14.3	24.7[a]	26.8[ab]	25.9[a]	30.5[b]	26.1
	s.d.	4.1	6.3	4.5	6.0	8.3	6.9
	Min	8.5	10.7	14.9	10.0	16.8	8.5
	Max	19.2	38.6	36.8	36.1	55.1	55.1
	% mean	54.9	94.5	102.6	99.3	117.0	
VOL09 (m^3)	Mean	0.04	0.21	0.22	0.24	0.40	0.25
	s.d.	0.03	0.15	0.11	0.14	0.33	0.20
	Min	0.01	0.01	0.03	0.01	0.06	0.01
	Max	0.07	0.62	0.47	0.58	1.58	1.58
	% mean	16.0	84.0	88.0	96.0	160.0	
HDR09	Mean	45.0	45.0	40.0	45.0	45.0	44.0
	s.d.	5.8	7.7	7.2	6.5	6.7	7.2
	Min	39.0	34.0	20.0	31.0	34.0	20.0
	Max	52.0	66.0	58.0	58.0	57.0	66.0
	% mean	102.3	102.3	90.9	102.3	102.3	

*When tiny groves were included in native grove area categorical analysis, tiny groves differed significantly from all other categories in HT09. No differences were detected among the other grove size categories.

Table 15. Candidate set of models of standardized 2009 height data for SEGI steckling grove samples as a function of native grove geographic characteristics. Full model included fixed effects of latitude of native grove of origin (Lat), area of native grove of origin (GA), native grove isolation by mean distance to two nearest sampled native groves in degrees latitude (Dist), and latitude-adjusted elevation (AdjEl). Model selection conducted using Akaike's information criterion (AIC). The best model is indicated by the lowest AIC value and the highest Akaike's weight (AIC_w). Bayesian Information Criterion (BIC) provided for comparison.

Model	df.resid	AIC	ΔAIC	BIC	Akaike's weights (AIC_w)	R^2_{adj}
GA + Dist	329	931.6	0.0	950.6	0.49	0.08
GA	328	932.4	0.8	947.6	0.33	0.07
GA + Dist+ AdjEl	327	933.5	1.9	956.4	0.19	0.08

Table 16. Candidate set of models of standardized 2009 height data for a subset of SEGI steckling grove samples from large and very large native groves as a function of native grove geographic characteristics. Full model included fixed effects for categorical harvest history (Harv), latitude of native grove of origin (Lat), area of native grove of origin (GA), native grove isolation by mean distance to two nearest sampled native groves in degrees latitude (Dist), and latitude-adjusted elevation (AdjEl). Model assessment conducted using Akaike's information criterion (AIC). The best model is indicated by the lowest AIC value and the highest Akaike's weight (AIC_w). Bayesian Information Criterion (BIC) provided for comparison.

Model	df.resid	AIC	ΔAIC	BIC	Akaike weights (AIC_w)	R^2_{adj}
Harv + AdjEl	158	474.3	0	489.8	0.36	0.08
AdjEl	159	475.7	1.40	488.0	0.18	0.08
Harv + GA	158	475.7	1.40	491.2	0.18	0.08
Harv+Dist+AdjEl	157	475.8	1.50	494.3	0.17	0.08
Harv	159	479.1	4.80	491.5	0.03	0.07
Lat	159	479.1	4.80	491.5	0.03	0.07
Harv+GA+Dist+Lat+AdjEl	155	479.2	4.90	503.9	0.03	0.07
Harv + Lat	158	480.8	6.50	496.3	0.01	0.07

Table 17. Descriptive statistics summarized for SEGI seedling tree height (m) in six measurement years from 1981 – 2009 by six SEGI seedling grove samples planted in trial 1 at Foresthill Seed Orchard.

		Height 1981				Height 1983				Height 1988			
Grove	n	Mean	s.d.	Max	Min	Mean	s.d.	Max	Min	Mean	s.d.	Max	Min
North Calaveras	14	0.22	0.06	0.33	0.13	0.93	0.24	1.41	0.54	2.8	0.57	4.2	1.6
Redwood Mtn	13	0.22	0.07	0.36	0.14	1.08	0.38	1.98	0.59	3.1	0.75	4.5	1.6
Giant Forest	14	0.21	0.05	0.30	0.15	1.08	0.24	1.46	0.60	3.0	0.48	3.9	2.3
Cedar Flat	13	0.16	0.04	0.25	0.12	0.94	0.31	1.61	0.44	3.1	0.79	4.6	1.7
Garfield	11	0.20	0.05	0.31	0.14	0.94	0.25	1.38	0.62	2.8	0.64	3.9	1.8
Mountain Home	14	0.22	0.08	0.42	0.13	0.99	0.33	1.38	0.38	2.8	0.70	3.7	1.4
Overall Mean	79	0.21	0.06	0.42	0.12	0.99	0.29	1.98	0.38	2.9	0.65	4.6	1.4
		Height 1991				Height 1997				Height 2009			
Grove	n	Mean	s.d.	Max	Min	Mean	s.d.	Max	Min	Mean	s.d.	Max	Min
North Calaveras	14	4.7	0.88	6.4	2.8	6.9	1.6	10.0	4.3	11.8	2.5	16.7	8.2
Redwood Mtn	13	5.2	1.25	8.0	3.0	8.0	1.9	11.2	4.2	14.0	3.4	19.6	7.9
Giant Forest	14	4.8	0.58	6.0	4.2	7.3	1.3	9.5	5.7	13.1	2.4	17.5	9.9
Cedar Flat	13	5.0	1.22	6.6	2.9	7.2	1.9	9.8	4.3	12.7	2.9	16.7	7.8
Garfield	11	4.7	0.75	5.9	3.5	7.2	1.2	9.0	5.6	13.8	2.6	19.9	10.9
Mountain Home	14	4.5	0.85	5.1	2.3	7.0	1.3	8.5	3.8	12.8	2.4	15.3	7.8
All	79	4.8	0.95	8.0	2.3	7.2	1.5	11.2	3.8	13.0	2.7	19.9	7.8

Table 18. Descriptive statistics summarized for SEGI seedling diameter at breat height (cm) and volume (m^3) in three measurement years from 1991 – 2009 by six SEGI seedling grove samples planted in trial 1 at Foresthill Seed Orchard.

		Diameter 1991				Diameter 1997				Diameter 2009			
Grove	n	Mean	s.d.	Max	Min	Mean	s.d.	Max	Min	Mean	s.d.	Max	Min
North Calaveras	14	11.9	3.7	21.5	5.2	19.4	4.1	29.0	14.0	30.3	6.2	42.8	22.2
Redwood Mtn	13	13.6	3.9	21.0	5.5	22.7	4.6	29.0	11.0	34.9	7.5	43.5	18.7
Giant Forest	14	12.4	2.4	15.4	8.9	21.9	3.7	28.0	14.0	33.1	5.7	40.1	24.1
Cedar Flat	13	13.1	4.4	19.2	4.0	20.9	5.3	29.0	9.0	32.7	6.6	41.0	15.6
Garfield	11	12.2	3.4	17.3	7.3	20.0	3.5	26.0	16.0	32.0	5.6	41.1	24.2
Mountain Home	14	11.2	4.1	16.8	3.2	19.5	4.3	25.0	11.0	31.7	6.9	40.9	17.9
Overall Mean	79	12.4	3.7	21.5	3.2	20.7	4.4	29.0	9.0	32.4	6.4	43.5	15.6

		Diameter 1991				Diameter 1997				Diameter 2009			
Grove	n	Mean	s.d.	Max	Min	Mean	s.d.	Max	Min	Mean	s.d.	Max	Min
North Calaveras	14	0.02	0.02	0.08	0.00	0.08	0.05	0.22	0.02	0.31	0.18	0.74	0.13
Redwood Mtn	13	0.03	0.02	0.09	0.00	0.12	0.06	0.25	0.01	0.50	0.27	0.91	0.07
Giant Forest	14	0.02	0.01	0.04	0.01	0.10	0.05	0.20	0.03	0.40	0.18	0.71	0.18
Cedar Flat	13	0.03	0.02	0.06	0.00	0.10	0.06	0.21	0.01	0.39	0.20	0.73	0.05
Garfield	11	0.02	0.01	0.04	0.00	0.08	0.04	0.15	0.04	0.40	0.22	0.88	0.19
Mountain Home	14	0.02	0.01	0.04	0.00	0.08	0.04	0.14	0.01	0.37	0.18	0.64	0.07
All	79	0.02	0.02	0.09	0.00	0.09	0.05	0.25	0.01	0.39	0.21	0.91	0.05

Table 19. Descriptive statistics summarized by six SEGI seedling grove samples in trial 1 for lower stem form traits fluting (FLUT), asymmetry (ASYM), and basal swelling (SWEL), crown fullness (FULL) and epicormic sprouting (EPI) after 29 growing seasons at Foresthill Seed Orchard in 2009. Traits scored on a scale of 0 – 3.

		FLUT				ASYM				SWEL			
Grove	n	Mean	s.d.	Max	Min	Mean	s.d.	Max	Min	Mean	s.d.	Max	Min
North Calaveras	14	0.9	0.7	2	0	2.0	0.7	3	1	2.4	0.5	3	2
Redwood Mtn	13	1.4	1.1	3	0	2.0	1.2	3	0	1.9	0.8	3	1
Giant Forest	14	1.9	1.1	3	0	2.2	1.1	3	0	1.9	0.6	3	1
Cedar Flat	13	1.4	1.0	3	0	2.2	0.8	3	1	1.6	0.7	3	1
Garfield	11	1.1	1.1	3	0	1.8	1.0	3	0	1.4	0.5	2	1
Mountain Home	14	1.3	1.3	3	0	2.1	1.0	3	0	1.7	0.6	3	1
Overall Mean	79	1.3	1.1	3	0	2.1	0.9	3	0	1.8	0.7	3	1

		FULL				EPI			
Grove	n	Mean	s.d.	Max	Min	Mean	s.d.	Max	Min
North Calaveras	14	1.4	0.94	3	0	0.1	0.3	1	0
Redwood Mtn	13	1.2	0.73	2	0	0.2	0.6	2	0
Giant Forest	14	1.6	0.85	3	0	0.0	0.0	0	0
Cedar Flat	13	1.8	0.99	3	0	0.2	0.8	3	0
Garfield	11	0.9	0.70	2	0	0.3	0.5	1	0
Mountain Home	14	1.0	1.04	3	0	0.1	0.3	1	0
All	79	1.3	0.92	3	0	0.1	0.5	3	0

Table 20. Descriptive statistics summarized for trial 2 mixed conifer seedling height (m) by species in six measurement years from 1981 to 2009 at Foresthill Seed Orchard. Species were incense-cedar (CADE), white fir (ABCO), Douglas-fir (PSME), sugar pine (PILA), ponderosa pine (PIPO), and giant sequoia (SEGI).

		CADE	ABCO	PSME	PILA	PIPO	SEGI	All
Year	n	33	13	15	19	33	32	145
1983	Mean	0.89	0.28	0.47	0.45	0.68	1.14	0.73
	s.d.	0.35	0.10	0.16	0.13	0.17	0.31	0.38
	Max	1.71	0.60	0.88	0.78	1.02	2.21	2.21
	Min	0.10	0.15	0.18	0.18	0.30	0.55	0.10
	% mean	123	39	65	62	94	157	
1986	Mean	2.3	0.9	1.5	1.6	2.3	2.8	2.0
	s.d.	0.8	0.4	0.5	0.5	0.5	0.7	0.8
	Max	3.8	2.2	2.5	2.5	3.7	5.8	5.8
	Min	0.4	0.1	0.3	0.3	1.2	1.1	0.1
	% mean	112	45	72	77	111	136	
1991	Mean	4.4	2.4	4.4	4.6	6.3	5.6	4.9
	s.d.	1.3	1.1	1.3	1.2	1.1	1.2	1.6
	Max	6.5	5.6	6.3	6.8	9.1	8.5	9.1
	Min	0.9	0.3	1.3	1.2	2.5	2.4	0.3
	% mean	90	49	90	96	129	115	
1997	Mean	5.4	4.3	7.4	7.7	9.7	7.5	7.2
	s.d.	1.7	1.9	1.6	2.0	1.4	1.8	2.4
	Max	8.6	9.2	10.4	11.2	12.8	11.8	12.8
	Min	1.0	0.9	2.8	2.1	4.5	3.5	0.9
	% mean	74	59	103	106	135	105	
2009	Mean	9.3	12.8	17.0	18.2	20.5	14.7	15.5
	s.d.	2.6	4.6	2.3	2.8	2.7	3.9	5.1
	Max	14.2	18.3	20.3	22.4	26.1	21.9	26.1
	Min	3.8	2.2	11.1	9.1	10.2	4.6	2.2
	% mean	60	83	110	117	132	95	

Table 21. Descriptive statistics summarized for trial 2 mixed conifer seedling stem diameter at breast height (cm) by species in three measurement years from 1991 to 2009 at Foresthill Seed Orchard. Species were incense-cedar (CADE), white fir (ABCO), Douglas-fir (PSME), sugar pine (PILA), ponderosa pine (PIPO), and giant sequoia (SEGI).

		CADE	ABCO	PSME	PILA	PIPO	SEGI	All
Year	n	33	13	15	19	33	32	145
1991	Mean	9.0	3.0	6.4	8.8	15.9	13.8	10.5
	s.d.	3.6	2.5	2.7	3.1	3.0	3.6	5.2
	Max	14.8	11.2	12.0	15.7	24.0	25.5	25.5
	Min	3.1	1.9	2.5	3.2	3.4	3.7	5.2
	% mean	86	28	61	84	151	131	
1997	Mean	12.8	7.6	14.5	17.4	26.5	20.2	17.6
	s.d.	4.0	4.2	4.1	5.0	4.7	4.7	7.3
	Max	20.0	19.0	22.0	26.0	38.0	33.0	38.0
	Min	3.5	4.1	3.8	5.3	4.7	5.1	7.6
	% mean	73	43	83	99	150	115	
2009	Mean	19.8	20.6	31.6	37.7	45.2	31.2	32.1
	s.d.	5.6	7.6	6.8	7.1	6.59	8.5	11.7
	Max	30.4	28.9	49.8	47.2	58	48.4	58.0
	Min	4.9	8.2	6.4	7.9	6.4	7.4	11.3
	% mean	62	64	99	118	141	97	

Table 22. Descriptive statistics summarized for trial 2 mixed conifer seedling conic stem volume (m^3) by species in three measurement years from 1991 to 2009 at Foresthill Seed Orchard. Species were incense-cedar (CADE), white fir (ABCO), Douglas-fir (PSME), sugar pine (PILA), ponderosa pine (PIPO), and giant sequoia (SEGI).

		CADE	ABCO	PSME	PILA	PIPO	SEGI	All
Year	n	33	13	15	19	33	32	145
1991	Mean	0.0140	0.0010	0.0070	0.0120	0.0480	0.0310	0.0231
	s.d.	0.0098	0.0009	0.0057	0.0093	0.0244	0.0202	0.0227
	Max	0.0370	0.0030	0.0210	0.0330	0.1190	0.0730	0.1191
	Min	0.0004	0.0000	0.0004	0.0000	0.0014	0.0009	0.0000
	% mean	61	4	30	52	208	134	
1997	Mean	0.0300	0.0070	0.0540	0.0750	0.2020	0.0960	0.0901
	s.d.	0.0194	0.0079	0.0314	0.0462	0.0834	0.0635	0.0858
	Max	0.0890	0.0240	0.1200	0.1690	0.4840	0.2380	0.4839
	Min	0.0018	0.0000	0.0080	0.0009	0.0170	0.0060	0.0000
	% mean	33	8	60	83	224	107	
2009	Mean	0.1380	0.1510	0.5580	0.7300	1.1280	0.4950	0.5642
	s.d.	0.0786	0.1194	0.2451	0.3119	0.3614	0.2895	0.4497
	Max	0.3000	0.3700	1.2270	1.3060	1.9900	1.2630	1.9904
	Min	0.0211	0.0007	0.2582	0.0595	0.1212	0.0550	0.0007
	% mean	24	27	99	129	200	88	

Table 23. Descriptive statistics summarized for trial 2 mixed conifer seedling height-diameter ratio (HDR) by species in three measurement years from 1991 to 2009 at Foresthill Seed Orchard. Species were incense-cedar (CADE), white fir (ABCO), Douglas-fir (PSME), sugar pine (PILA), ponderosa pine (PIPO), and giant sequoia (SEGI).

		CADE	ABCO	PSME	PILA	PIPO	SEGI	All
Year	n	33	13	15	19	33	32	145
1991	Mean	50.0	105.0	70.0	59.0	40.0	42.0	53.0
	s.d.	53.0	10.9	11.8	20.9	4.2	5.4	24.1
	Max	228.6	96.2	92	140	54.3	63.2	228.6
	Min	62.1	35.6	46.7	43.7	29.7	33.6	29.7
	% mean	94	199	131	111	76	80	
1997	Mean	42	65	51	45	37	38	43.0
	s.d.	31.8	5.7	7.0	5.6	2.9	3.7	12.4
	Max	160	56	65.4	61.7	44.0	45.0	160
	Min	46.7	30.6	42.6	37.3	31.3	29.5	29.5
	% mean	98	152	119	105	85	88	
2009	Mean	48	63	53	50	46	48	50.0
	s.d.	5.8	4.5	8.0	5.4	3.6	3.7	6.8
	Max	73.1	57.9	68.7	61.3	53.1	57.7	73.1
	Min	51.0	40.5	38.0	37.7	39.0	39.0	37.7
	% mean	96	127	107	101	92	97	

Table 24. Candidate set of competition indices (CI) predicting SEGI stem diameter at breast height (DBH) increment (mm yr^{-1}) as a response to neighborhood mixed conifer competition from seven meter to 11 meter neighborhood radii centered on the subject tree in the growth period 1997 to 2009. Models are ranked by AIC_c (lowest is best). Akaike's weights indicate the likelihood that a model is the best model of the candidate models (highest is best). ln = natural logarithm of the calculated CI value for each subject tree. RMSE = root mean square error (mm) of predictions of mean annual DBH increment. CIs defined in Table 3.

Model	df	RMSE	AIC	AICc	ΔAICc	Akaike Weights	$adjR^2$
$lnCIDBH^2$ 7m	35	1.82	173.33	173.96	0.00	0.38	0.64
$lnCIDBH^2$ 10m	35	1.82	173.43	174.06	0.10	0.36	0.64
lnCIHeg 7m	35	1.84	174.39	175.02	1.06	0.22	0.63
CIHeg 7m	35	1.93	178.27	178.90	4.94	0.03	0.60
$CIDBH^2$ 7m	35	1.99	180.92	181.55	7.59	0.01	0.57
$CIDBH^2$ 10m	35	2.03	182.64	183.28	9.32	0.00	0.55
$CIDist^2$ 11m	35	2.05	183.46	184.09	10.13	0.00	0.55
NULL	35	3.04	215.67	215.98	42.02	0.00	

Table 25. Candidate set of competition indices (CI) predicting SEGI stem diameter at breast height (DBH) increment (mm yr^{-1}) as a response to seven meter radius neighborhood competition centered on the subject tree by individual species sums in the growth period 1997 to 2009. Models are ranked by AICc (lowest is best). Akaike's weights indicate the likelihood that a model is the best model of the candidate models (highest is best). Species included in full model were incense-cedar (CADE), white fir (ABCO), Douglas-fir (PSME), sugar pine (PILA), ponderosa pine (PIPO), and giant sequoia (SEGI). ln = natural logarithm of the calculated CI value for each subject tree. RMSE = root mean square error (mm) of predictions of mean annual DBH increment. CIs defined in Table 3.

Model	df	RMSE	AIC	AICc	ΔAICc	Akaike Weights	$adjR^2$
lnCIHeg 7m no PILA, no PSME	37	1.80	175.42	177.81	0.00	0.34	0.65
lnCIHeg 7m no PILA	36	1.79	175.51	178.81	0.99	0.21	0.66
lnCIDBH^2 7m no PILA, no PSME	37	1.84	176.91	179.31	1.50	0.16	0.64
CIHeg 7m no PILA, no PSME	36	1.83	177.53	180.82	3.01	0.08	0.64
lnCIDBH^2 7m no PILA, no PSME	37	1.87	178.24	180.64	2.82	0.08	0.62
lnCIDBH^2 7m no PILA, no PSME, no CADE	38	1.92	179.88	181.55	3.73	0.05	0.60
lnCIHeg 7m FULL	35	1.81	177.42	181.78	3.96	0.05	0.65
lnCIDBH^2 7m FULL	35	1.85	179.31	183.67	5.86	0.02	0.63
lnCIHeg 7m no ABCO	36	2.12	189.75	193.04	11.94	0.00	0.52

Table 26. Descriptive statistics summarized for trial 3 SEGI seedling and mixed conifer seedling tree size traits height (m) (HT09), diameter at breast height (cm) (DBH09), conic stem volume (m^3) (VOL09), and height-diameter ratio (HDR) by species planted on three brush competition treatments after 29 growing seasons Foresthill Seed Orchard. Species included in full model were incense-cedar (CADE), white fir (ABCO), Douglas-fir (PSME), sugar pine (PILA), ponderosa pine (PIPO), and giant sequoia (SEGI).

Year		CADE	ABCO	PSME	PILA	PIPO	SEGI	All
	n	15	17	18	18	17	71	156
HT09	Mean	3.7	12.3	14.9	16.1	18.4	11.5	12.5
	s.d.	3.4	1.7	3.0	3.3	2.7	3.2	4.8
	Max	8.0	17.2	18.2	20.3	24.1	21.5	24.1
	Min	1.5	4.3	8.1	6.1	14.3	3.5	1.5
	% mean	30	98	119	129	147	92	100
DBH09	Mean	5.6	19.8	25.7	30.4	35.9	20.0	22.2
	s.d.	3.6	5.9	7.9	8.4	5.9	7.0	10.2
	Max	14.3	30.7	38.6	42.6	45.5	54	54
	Min	0.3	8.9	13.6	10.9	23.6	6.5	0.3
	% mean	25	89	116	137	162	90	100
VOL09	Mean	0.01	0.15	0.30	0.45	0.66	0.16	0.25
	s.d.	0.01	0.12	0.21	0.27	0.28	0.21	0.28
	Max	0.04	0.39	0.70	0.96	1.31	1.64	1.64
	Min	0.00	0.05	0.05	0.02	0.21	0.00	0.00
	% mean	4	60	120	180	264	64	100
HDR09	Mean	62.2	104.5	60.6	54.2	51.9	58.6	62.4
	s.d.	6.9	112.8	12.5	6.5	5.8	8.0	37.5
	Max	73.3	500	87.4	64.1	63.6	84.5	500
	Min	48.3	51.5	41.1	42.6	39.4	39.8	39.4
	% mean	99.7	167.5	97.1	86.9	83.2	93.9	100.0

Table 27. Generalized linear mixed effects model fixed treatment effects and interactions for SEGI seedling and mixed conifer stem volume (m^3) in 2009 planted at stand edge and interior locations with three brush treatments: *Ceanothus*, *Arctostaphylos*, and bare ground in trial 3 after 29 growing seasons at Foresthill Seed Orchard.

Effect	df	Den df	F-value	Pr > F
Species	5	141	21.80	0.0001
Treatment	2	141	15.46	0.0001
Edge	1	141	3.78	0.0539
Species x Treatment	10	141	2.53	0.0078
Species x Edge	5	141	5.70	0.0001

Table 28. Generalized linear mixed effects model treatment effects (effect slices) by species for SEGI seedling and mixed conifer species stem volume (m^3) in 2009 planted at edge and interior locations with three brush treatments: *Ceanothus*, *Arctostaphylos*, and bare ground in trial 3 after 29 growing seasons at Foresthill Seed Orchard. Species were incense-cedar (CADE), white fir (ABCO), Douglas-fir (PSME), sugar pine (PILA), ponderosa pine (PIPO), and giant sequoia (SEGI).

Effect	df	Den df	F-value	Pr > F
ABCO	2	141	0.34	0.7112
CADE	2	141	0.00	1.0000
PSME	2	141	3.58	0.0304
PILA	2	141	9.66	0.0001
PIPO	2	141	10.96	0.0001
SEGI	2	141	2.34	0.0998

Table 29. Descriptive statistics summarized for heartwood decay resistance (Decay) and stem diameter at breast height (DBH97) of SEGI seedling stumps (n = 139) thinned in 1999 by seedling grove sample at Foresthill Seed Orchard. Heartwood decay was evaluated on a four point scale (0 = mostly decayed; 3 = decay resistant) in 2010, 11 years after thinning in 1999.

	Decay						DBH97				
Grove	n	Mean	s.d.	Max	Min	%mean	Mean	s.d.	Max	Min	%mean
North Calaveras	25	2.1	0.6	3	1	101	18.3	3.5	25	12	91
Redwood Mtn	21	2.2	0.7	3	1	106	21.0	2.5	26	17	104
Giant Forest	22	1.9	0.8	3	0	94	20.0	5.0	29	11	99
Cedar Flat	17	2.1	0.8	3	0	102	20.8	4.2	29	10	103
Garfield	26	2.1	0.7	3	1	104	19.9	3.9	30	13	98
Mountain Home	28	1.9	0.7	3	1	93	21.2	4.1	31	14	105
All		2.1	0.7	3	0		20.3	4.0	31	10	100

Table 30. Descriptive statistics summarized for heartwood decay resistance (Decay) and stem diameter at breast height (DBH97) of SEGI standard clone stumps (n = 102) thinned in 1999 by standard clone grove sample at Foresthill Seed Orchard. Heartwood decay was evaluated on a four point scale (0 = mostly decayed; 3 = decay resistant) in 2010, 11 years after thinning in 1999.

		Decay					DBH97				
Grove	n	Mean	s.d.	Max	Min	% mean	Mean	s.d.	Max	Min	% mean
North Calaveras	10	2.1	0.9	3	1	106	16.0	1.6	19.0	13.0	98
Merced	11	1.9	0.7	3	1	96	14.5	2.7	19.0	10.0	89
Merced 2	20	1.6	0.9	3	0	81	18.3	3.7	27.0	8.0	112
Grant	14	1.9	1.0	3	0	97	12.9	3.6	22.0	12.0	79
Windy Gulch	13	1.8	0.7	3	1	93	15.9	3.6	26.0	11.0	98
Cedar Flat	4	1.8	0.5	2	1	88	15.3	2.6	19.0	11.0	94
Cedar Flat 2	15	2.3	0.7	3	1	114	17.5	4.6	27.0	8.0	107
Mountain Home	15	2.4	0.5	3	2	121	17.7	4.9	25.0	6.0	109
All		2.0	0.8	3	0		16.3	4.1	27.0	10	100

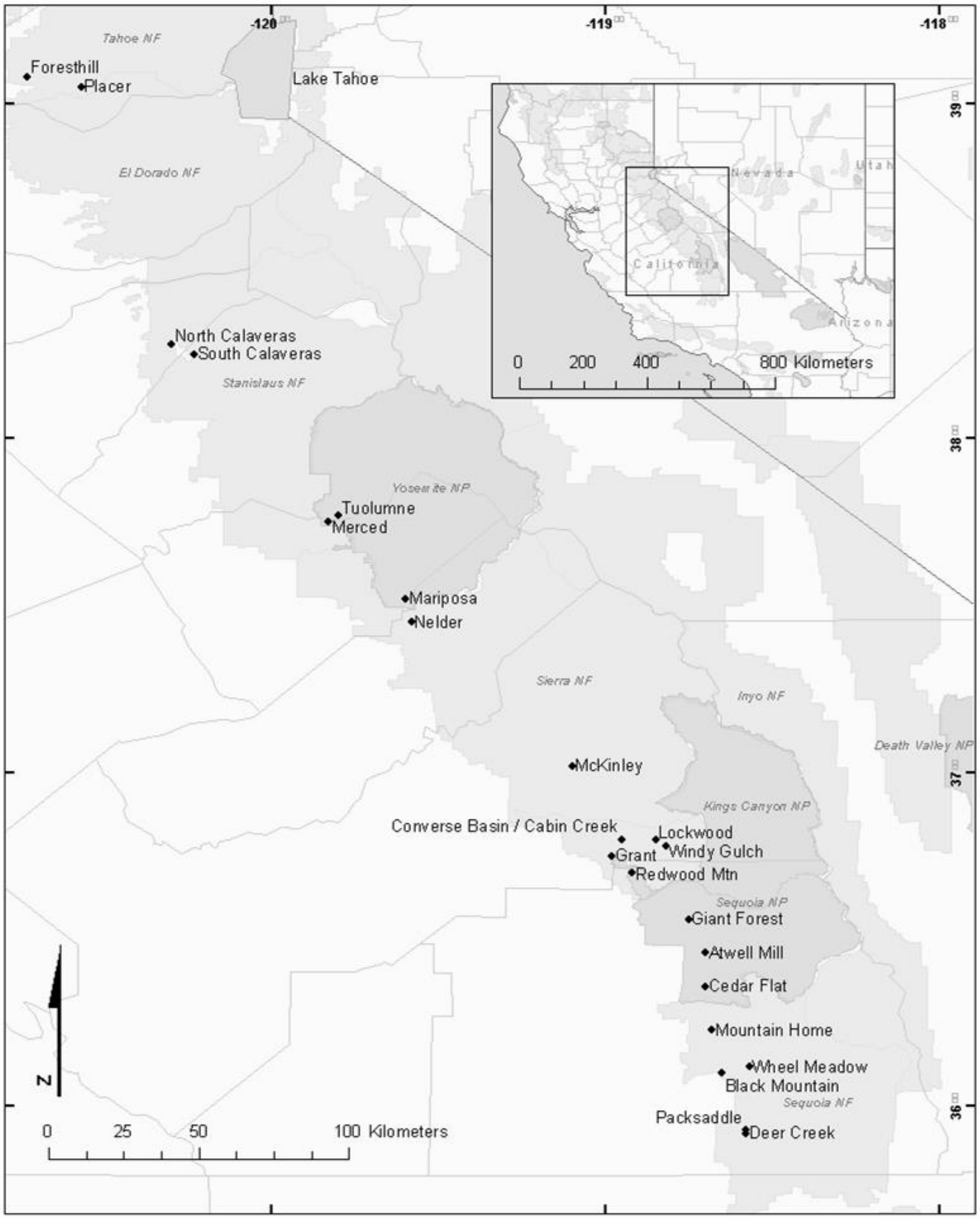


Figure 1. Map of 23 sampled SEGI native groves with progeny planted at Foresthill Seed Orchard study site. Foresthill Seed Orchard is located north of the northernmost native SEGI grove.

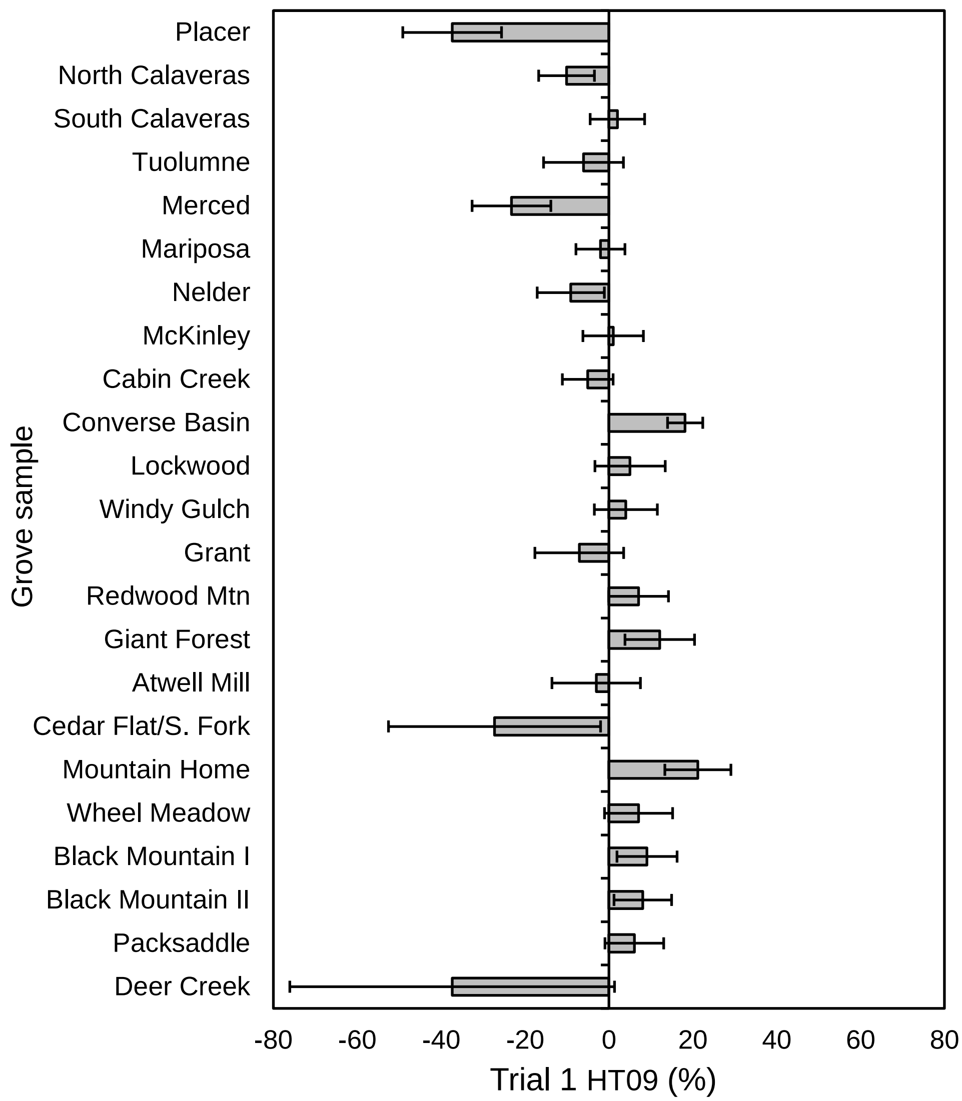


Figure 2. Trial 1 SEGI steckling grove sample mean height (HT09) in percent above or below the steckling mean after 29 growing seasons at Foresthill Seed Orchard as of 2009. Among-grove differences were statistically significant ($p \leq 0.05$) in a Kruskal-Wallis test. Placer and Deer Creek grove samples were not included in the analysis. Error bars are relative standard errors of the grove sample mean, where the grove sample standard error is divided by the mean and expressed as a percent (%). Grove samples arranged from north to south in the figure.

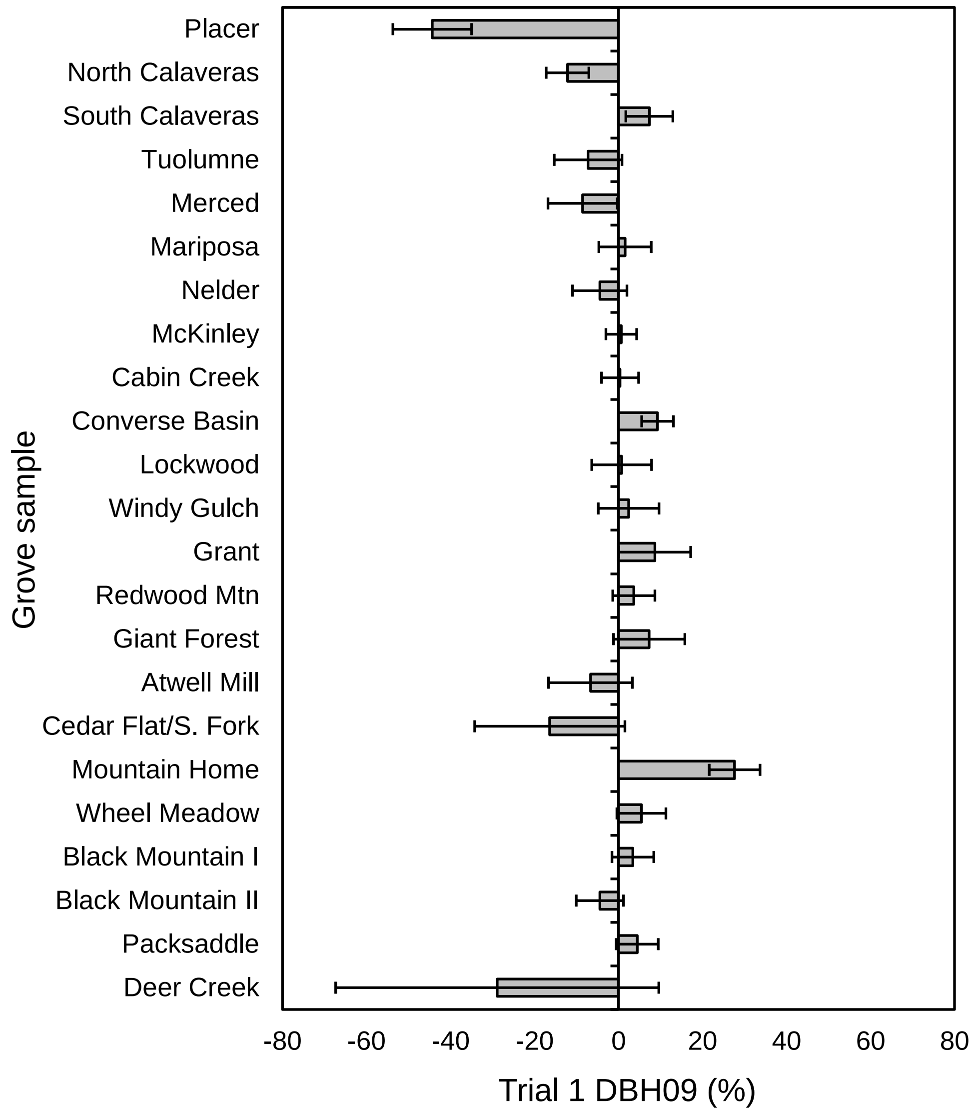


Figure 3. Trial 1 SEGI steckling grove sample mean diameter at breast height (DBH09) in percent above or below the steckling mean after 29 growing seasons at Foresthill Seed Orchard as of 2009. Among-grove differences were statistically significant ($p \leq 0.1$) in a Kruskal-Wallis test at alpha = 0.1. Placer and Deer Creek grove samples were not included in the analysis. Error bars are relative standard errors of the grove sample mean, where the grove sample standard error is divided by the mean and expressed as a percent (%). Grove samples arranged from north to south in the figure.

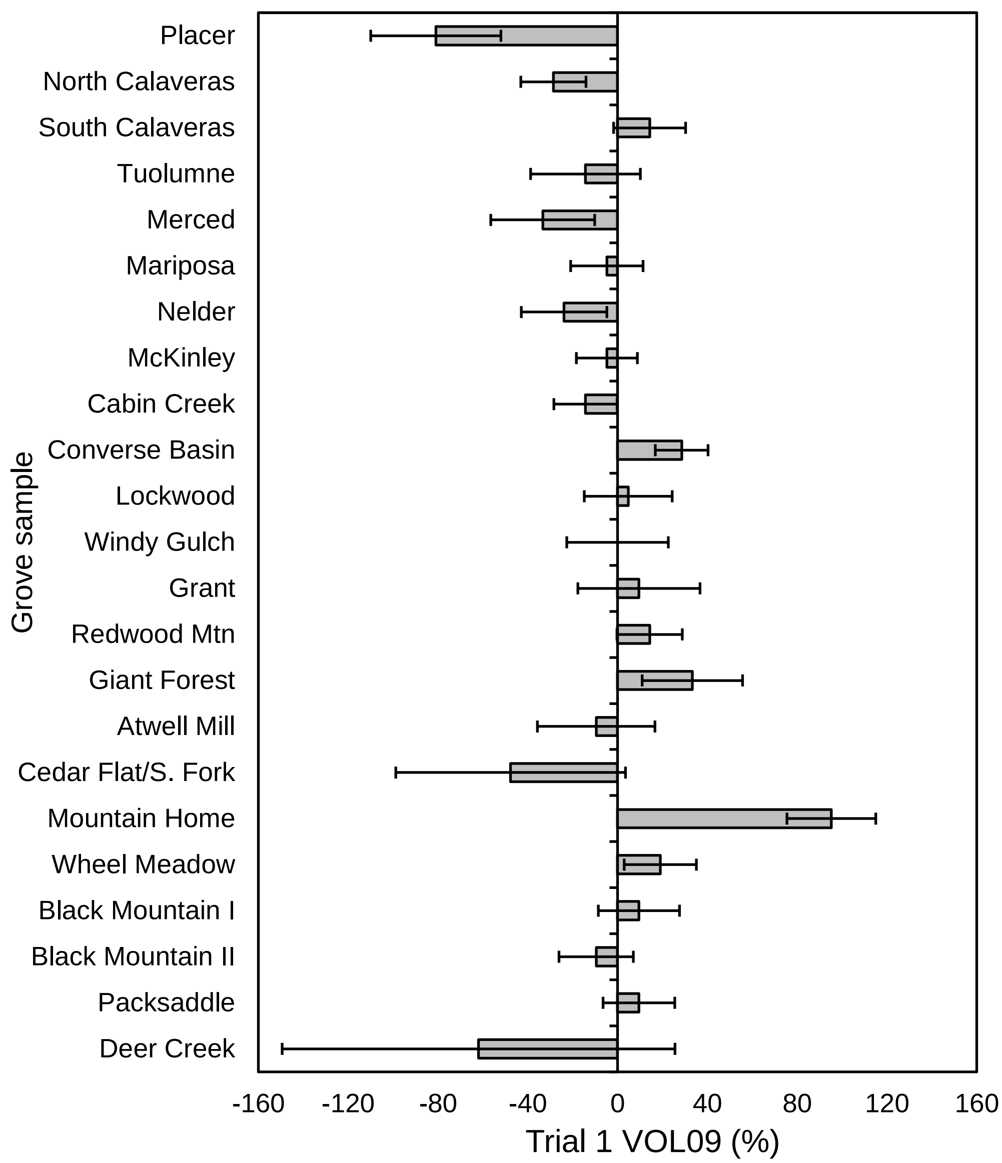


Figure 4. Trial 1 SEGI steckling grove sample mean stem volume (VOL09) in percent above or below the steckling mean after 29 growing seasons at Foresthill Seed Orchard as of 2009. Among-grove differences were statistically significant ($p \leq 0.1$) in a Kruskal-Wallis one way ANOVA at alpha = 0.1. Placer and Deer Creek grove samples were not included in the analysis. Error bars are relative standard errors of the grove sample mean, where the grove sample standard error is divided by the mean and expressed as a percent (%). Grove samples arranged from north to south in the figure.

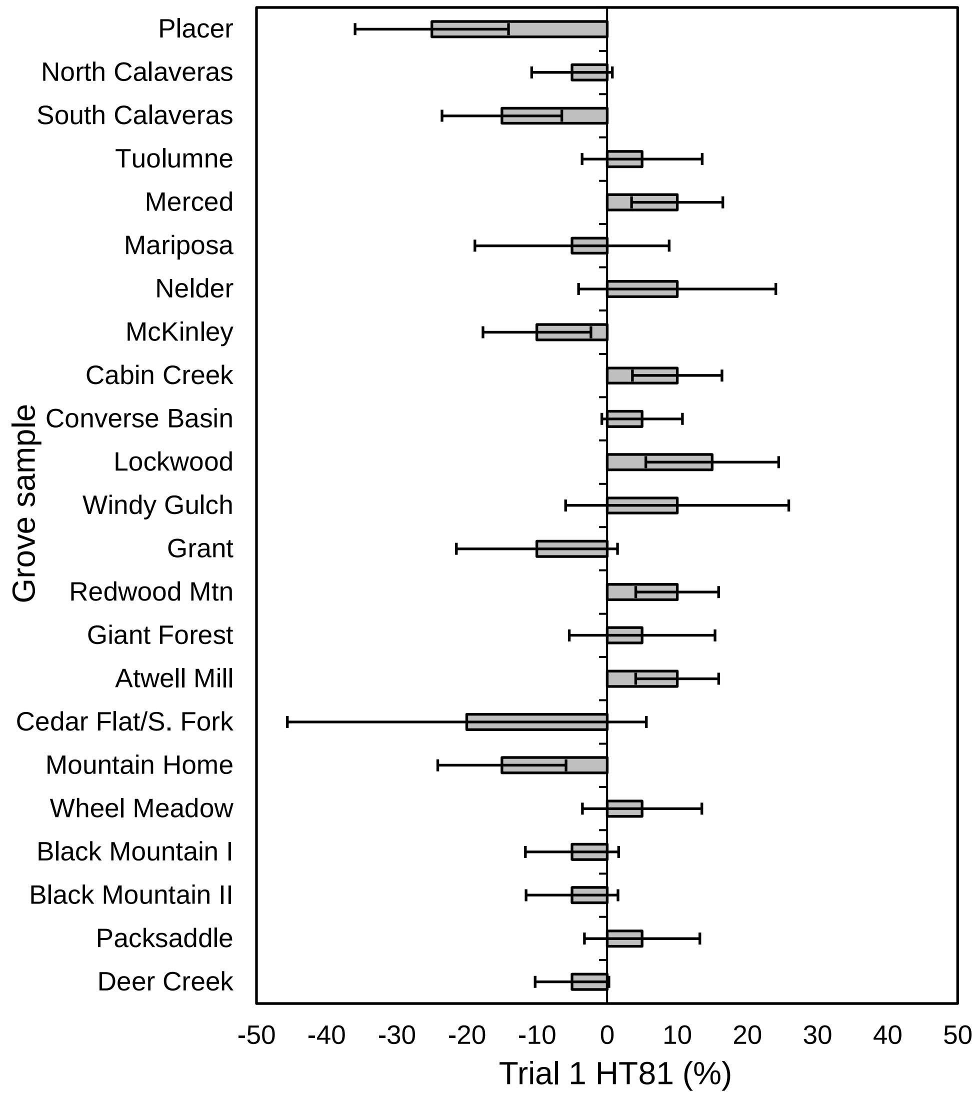


Figure 5. Trial 1 SEGI steckling grove sample mean height (HT81) in percent above or below the steckling mean after one growing seasons at Foresthill Seed Orchard as of 1981. Error bars are relative standard errors of the grove sample mean, where the grove sample standard error is divided by the mean and expressed as a percent (%). Grove samples arranged from north to south in the figure.

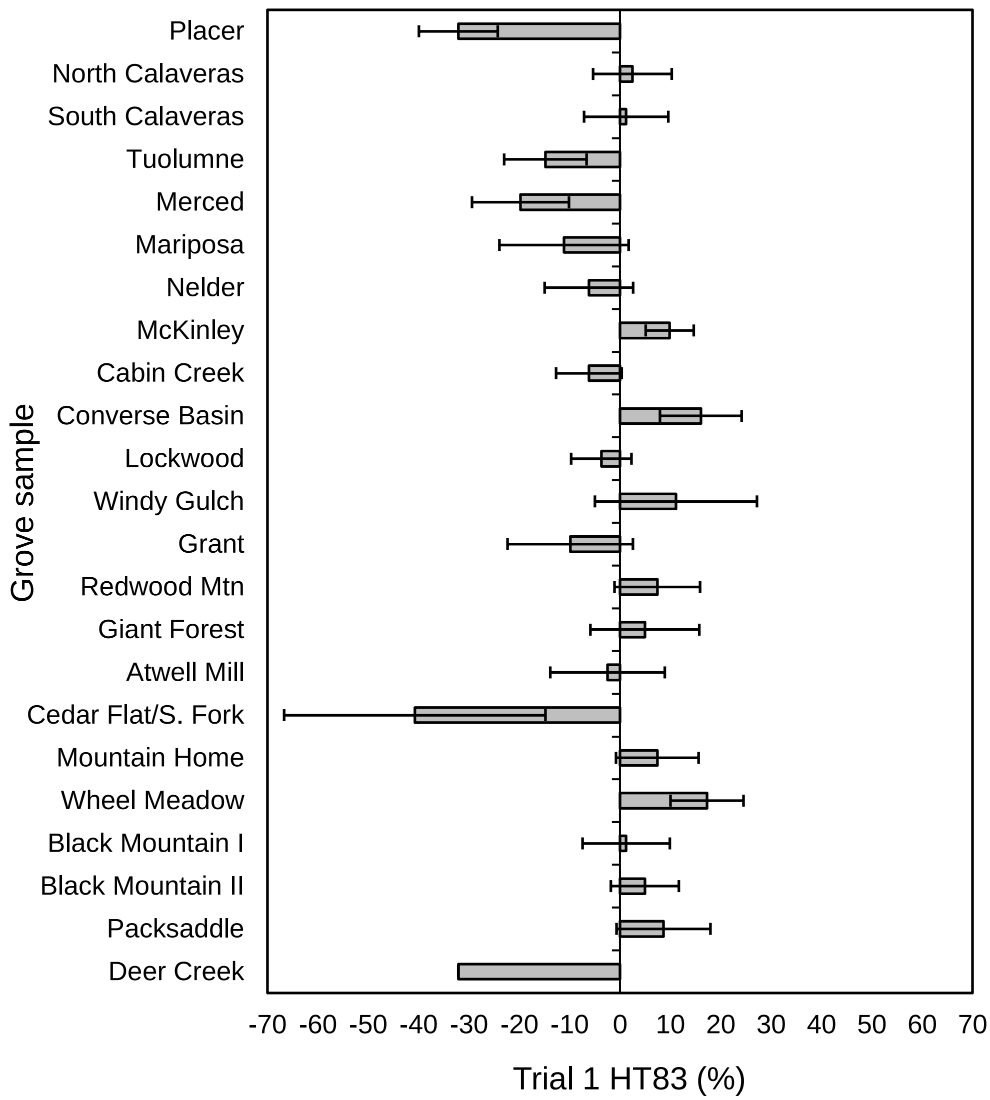


Figure 6. Trial 1 SEGI steckling grove sample mean height (HT83) in percent above or below the steckling mean after three growing seasons at Foresthill Seed Orchard as of 1983. Error bars are relative standard errors of the grove sample mean, where the grove sample standard error is divided by the mean and expressed as a percent (%). Grove samples arranged from north to south in the figure.

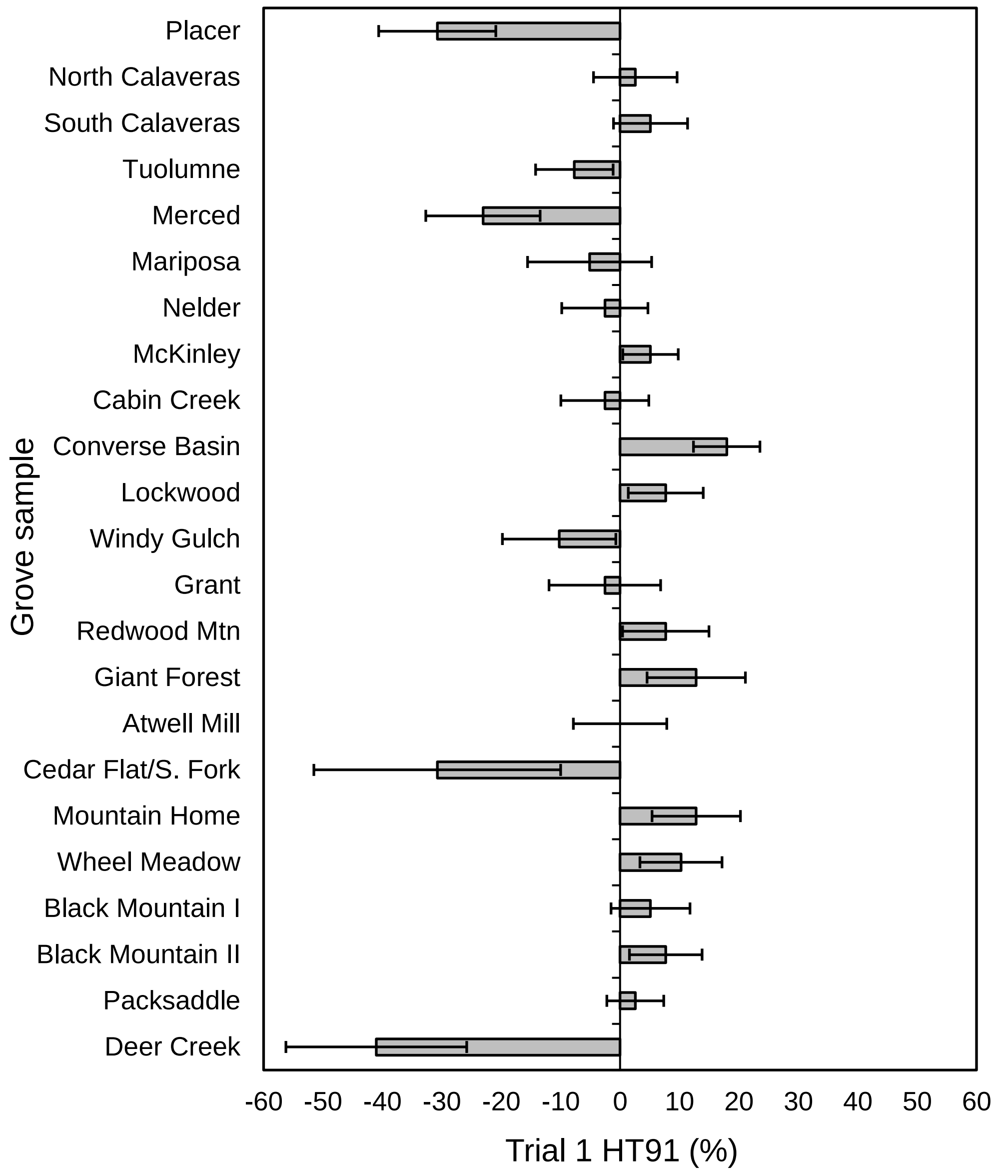


Figure 7. Trial 1 SEGI steckling grove sample mean height (HT91) in percent above or below the steckling mean after eleven growing seasons at Foresthill Seed Orchard as of 1991. Error bars are relative standard errors of the grove sample mean, where the grove sample standard error is divided by the mean and expressed as a percent (%). Grove samples arranged from north to south in the figure.

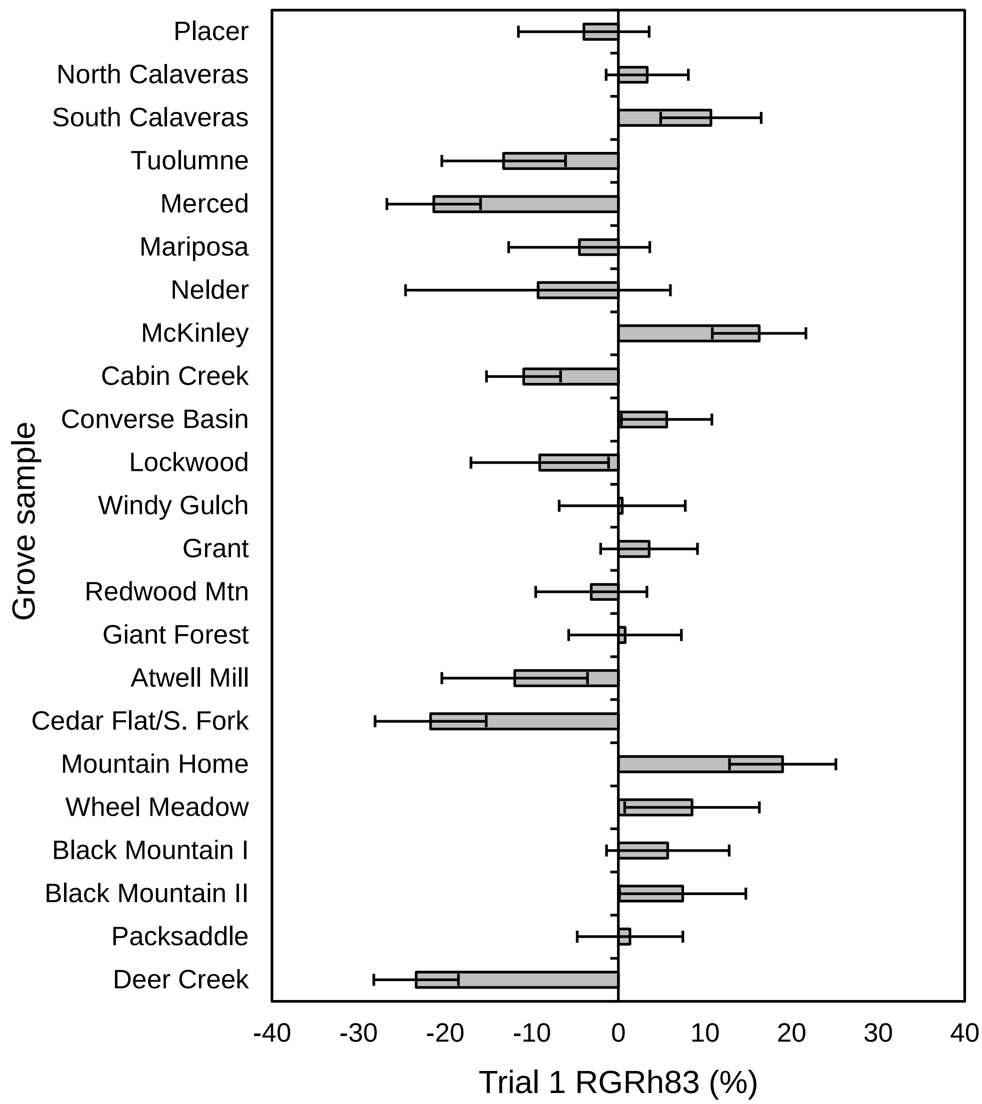


Figure 8. Trial 1 SEGI steckling grove sample mean relative height growth rate (RGRh) over two growing seasons at Foresthill Seed Orchard from 1981 to 1983 in percent above or below the overall mean. Among-grove differences were statistically significant ($p \leq 0.01$) in a Kruskal-Wallis one way ANOVA. Placer and Deer Creek grove samples were not included in analysis. Error bars are relative standard errors of the grove sample mean, where the grove sample standard error is divided by the mean and expressed as a percent (%). Grove samples arranged from north to south in the figure.

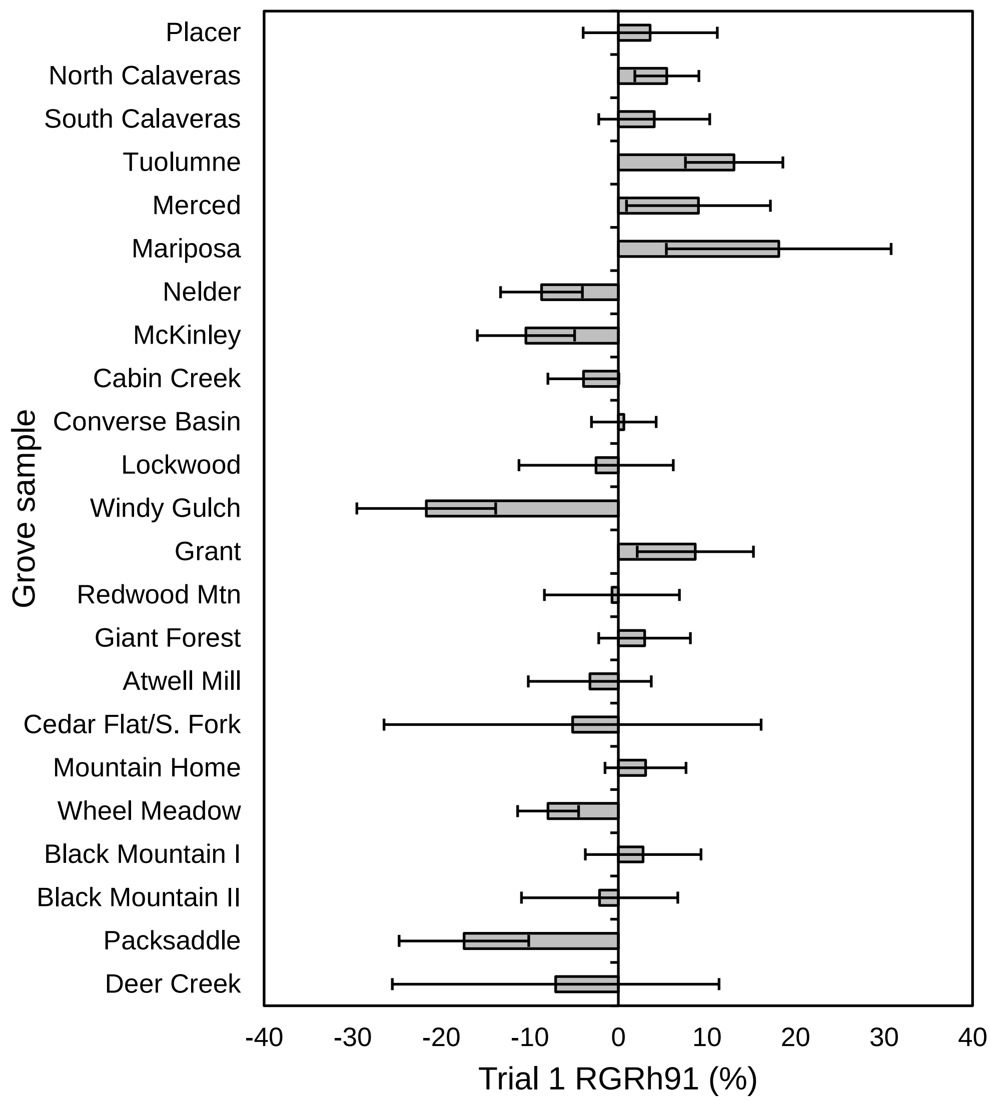


Figure 9. Trial 1 SEGI steckling grove sample mean relative height growth rate (RGRh) over three growing seasons at Foresthill Seed Orchard from 1988 to 1991 in percent above or below the overall mean. Among-grove differences were statistically significant ($p \leq 0.05$) in a Kruskal-Wallis non-parametric test. Placer and Deer Creek grove samples were not included in analysis. Error bars are relative standard errors of the grove sample mean, where the grove sample standard error is divided by the mean and expressed as a percent (%). Grove samples arranged from north to south in the figure.

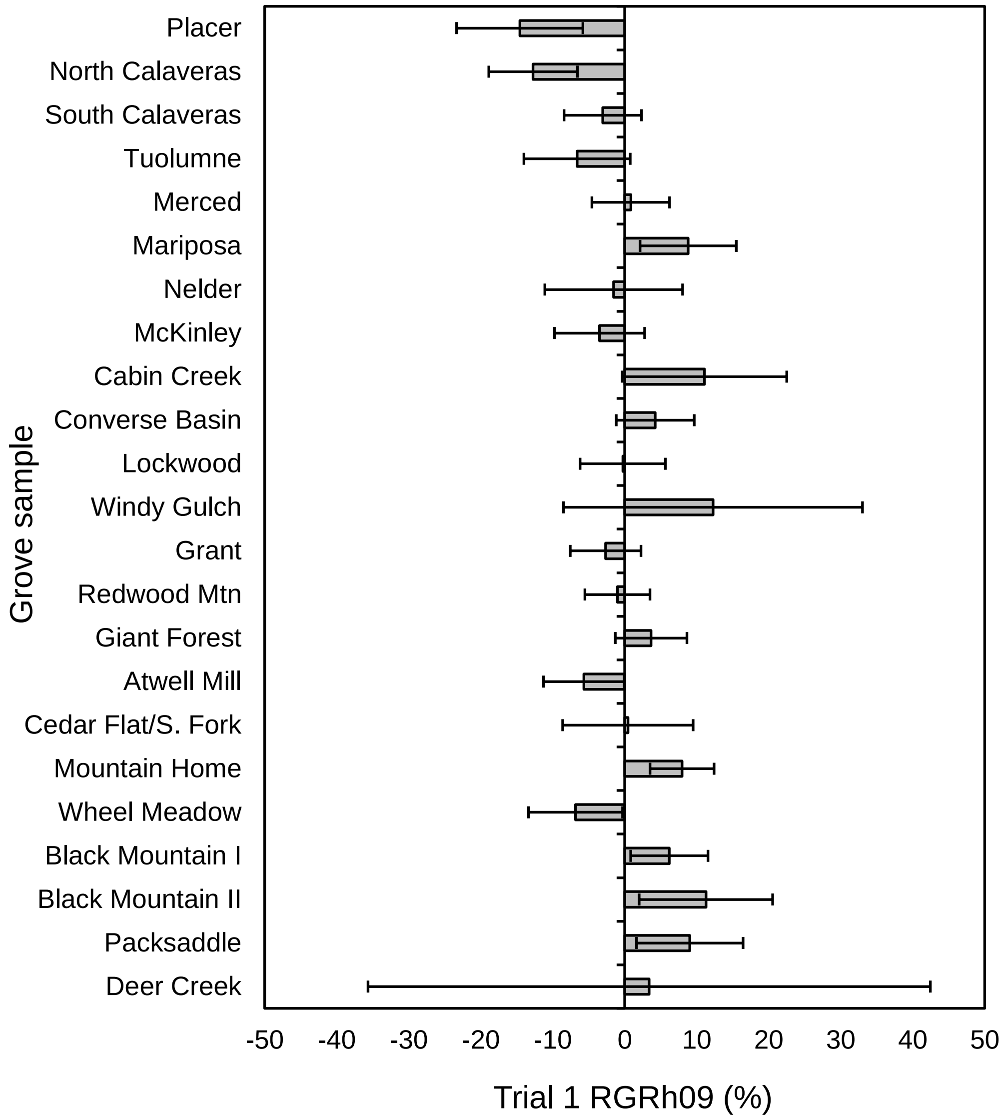


Figure 10. Trial 1 SEGI steckling grove sample mean relative height growth rate (RGRh) over three growing seasons at Foresthill Seed Orchard from 1997 to 2009 in percent above or below the overall mean. Error bars are relative standard errors of the grove sample mean, where the grove sample standard error is divided by the mean and expressed as a percent (%). Grove samples arranged from north to south in the figure.

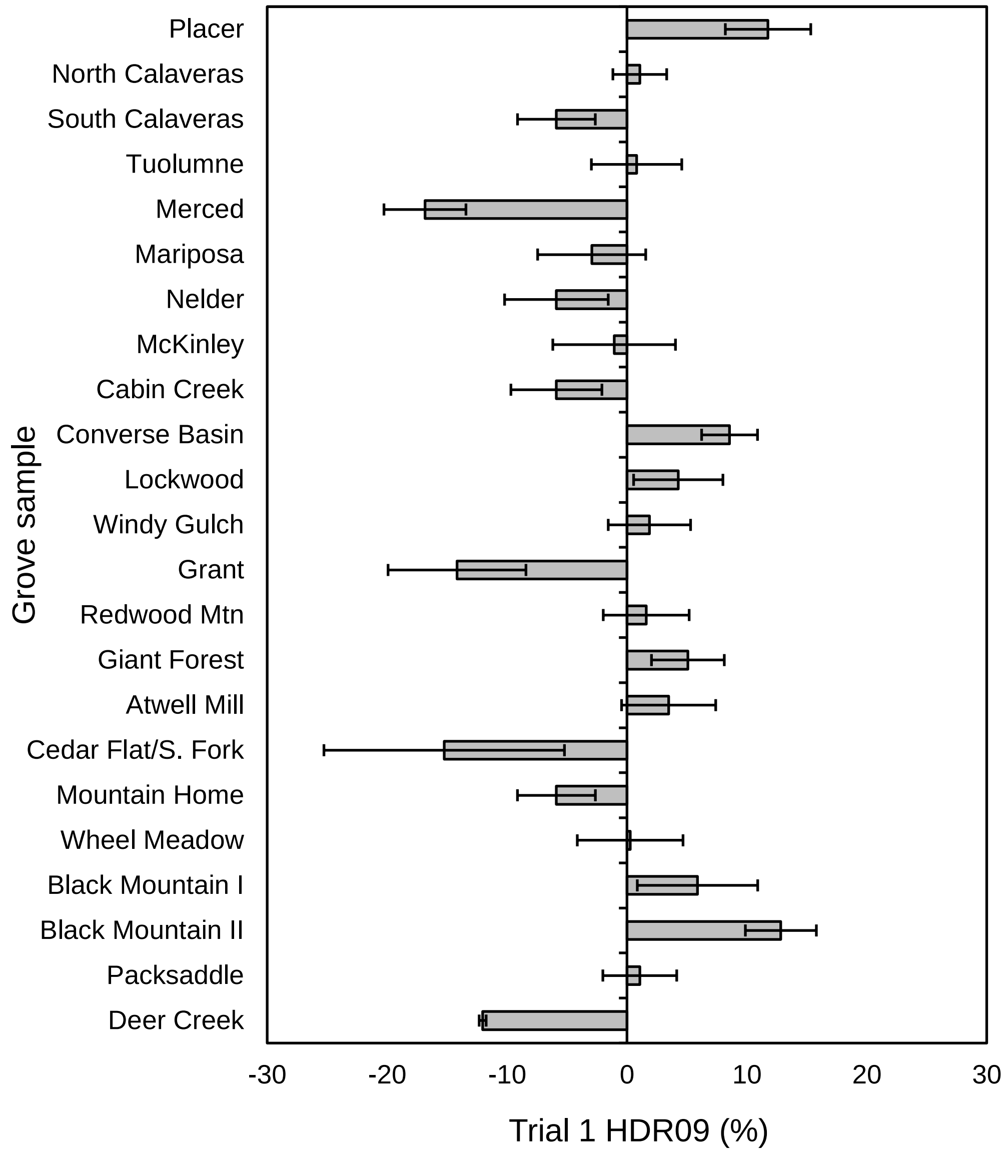


Figure 11. Trial 1 SEGI steckling grove sample mean height-diameter ratio (HDR) in percent above or below the within trial steckling mean after 29 growing seasons at Foresthill Seed Orchard as of 2009. Among-grove differences were statistically significant ($p \leq 0.0001$) in a Kruskal-Wallis one way ANOVA. Placer and Deer Creek grove samples were not included in analysis. Error bars are relative standard errors of the grove sample mean, where the grove sample standard error is divided by the mean and expressed as a percent (%). Grove samples arranged from north to south in the figure.

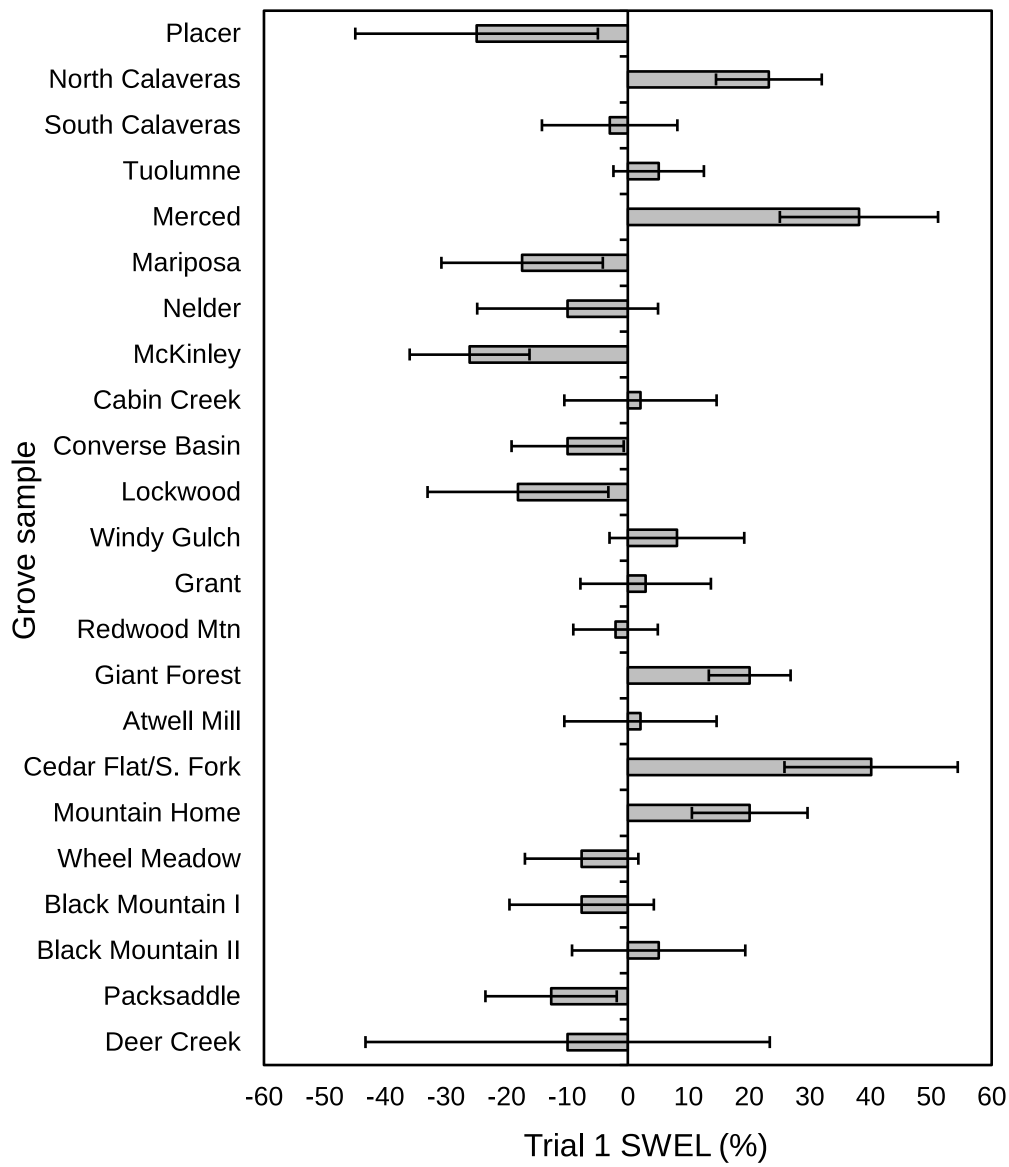


Figure 12. Trial 1 SEGI steckling grove sample basal swelling (SWEL) in percent above or below the steckling mean at Foresthill Seed Orchard after 29 growing seasons. Among-grove differences were statistically significant ($p \leq 0.01$) in a Kruskal-Wallis one way ANOVA. Placer and Deer Creek grove samples were not included in analysis. Error bars are relative standard errors of the grove sample mean, where the grove sample standard error is divided by the mean and expressed as a percent (%). Grove samples arranged from north to south in the figure.

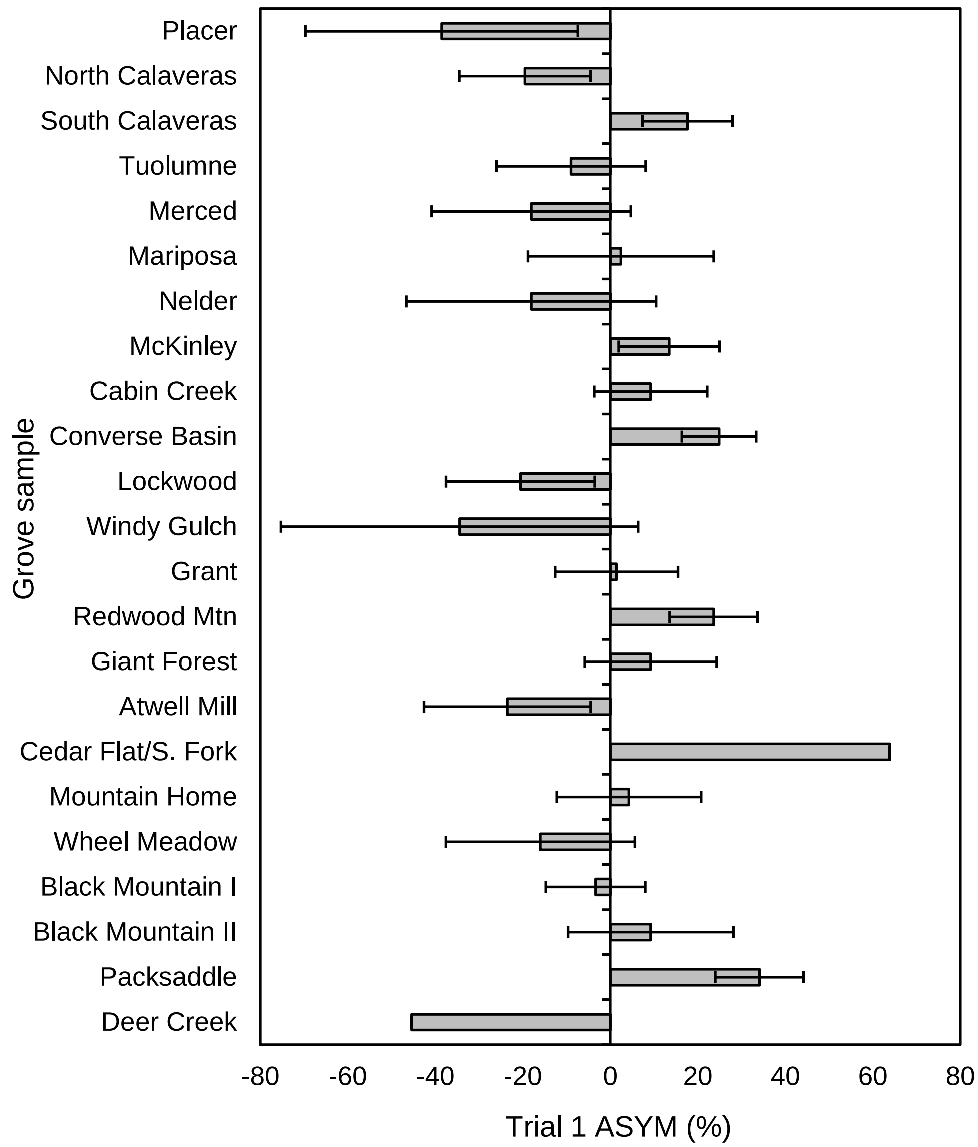


Figure 13. Trial 1 SEGI steckling grove sample lower stem asymmetry (ASYM) in percent above or below the overall mean at Foresthill Seed Orchard after 29 growing seasons. Among-grove differences were moderately significant ($p \leq 0.1$) in a Kruskal-Wallis one way ANOVA. Placer and Deer Creek grove samples were not included in analysis. Error bars are relative standard errors of the grove sample mean, where the grove sample standard error is divided by the mean and expressed as a percent (%). Grove samples arranged from north to south in the figure.

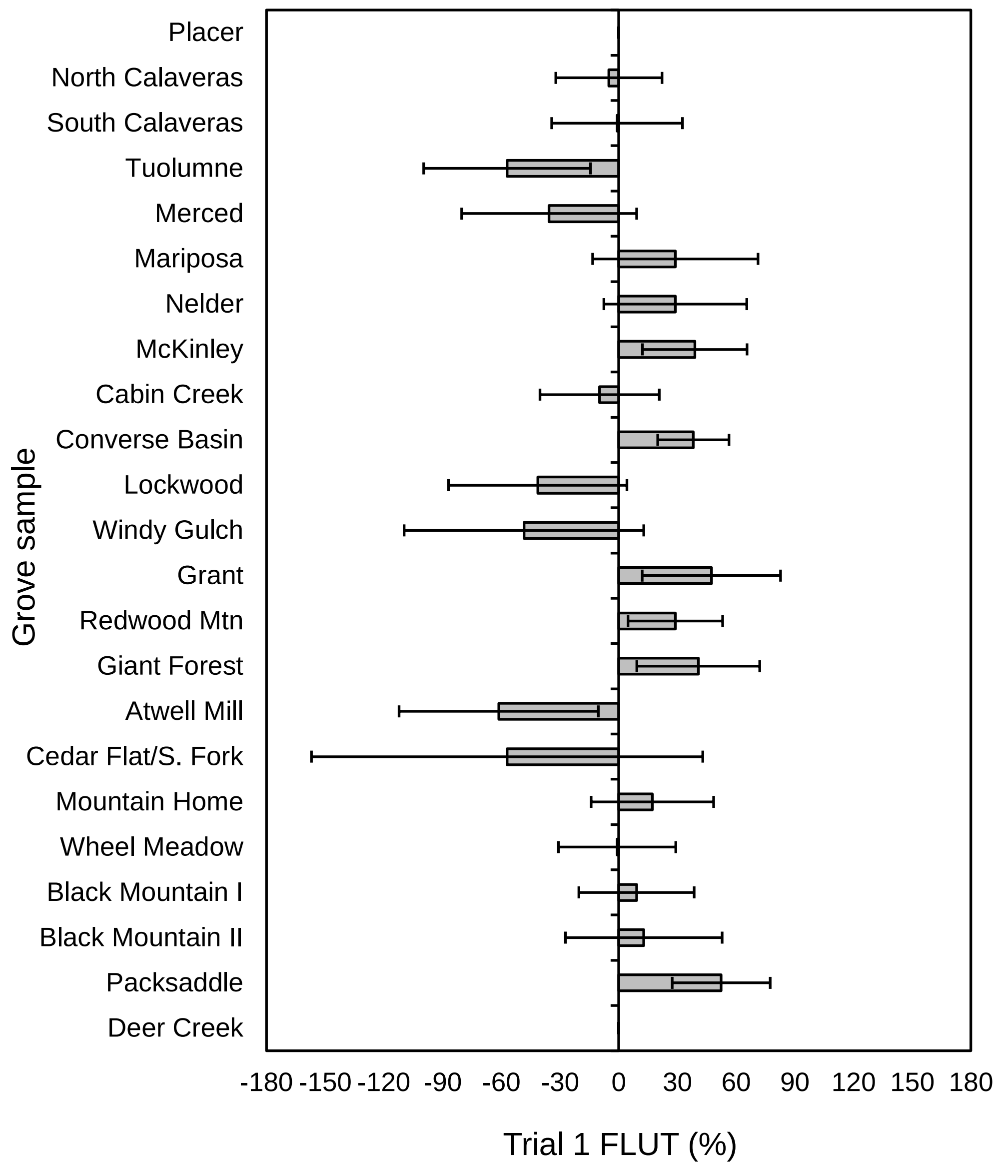


Figure 14. Trial 1 SEGI steckling grove sample lower stem fluting (FLUT) in percent above or below the overall mean at Foresthill Seed Orchard after 29 growing seasons. There was no FLUT observed in Placer or Deer Creek grove samples. Error bars are relative standard errors of the grove sample mean, where the grove sample standard error is divided by the mean and expressed as a percent (%). Grove samples arranged from north to south in the figure.

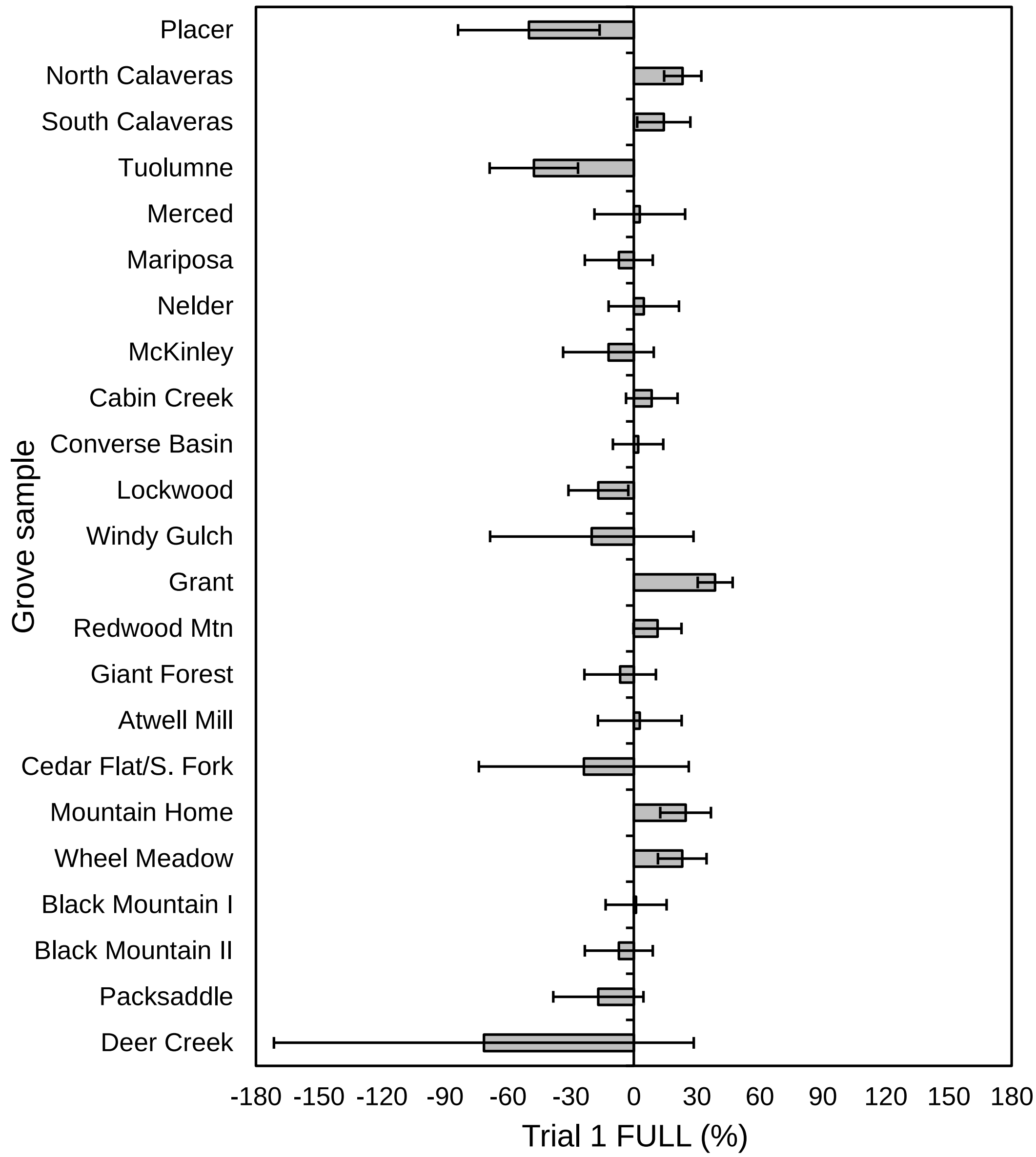


Figure 15. Trial 1 SEGI steckling grove sample crown fullness (FULL) in % above or below the overall steckling mean at Foresthill Seed Orchard after 29 growing seasons. Error bars are relative standard errors of the grove sample mean, where the grove sample standard error is divided by the mean and expressed as a percent (%). Grove samples arranged from north to south in the figure.

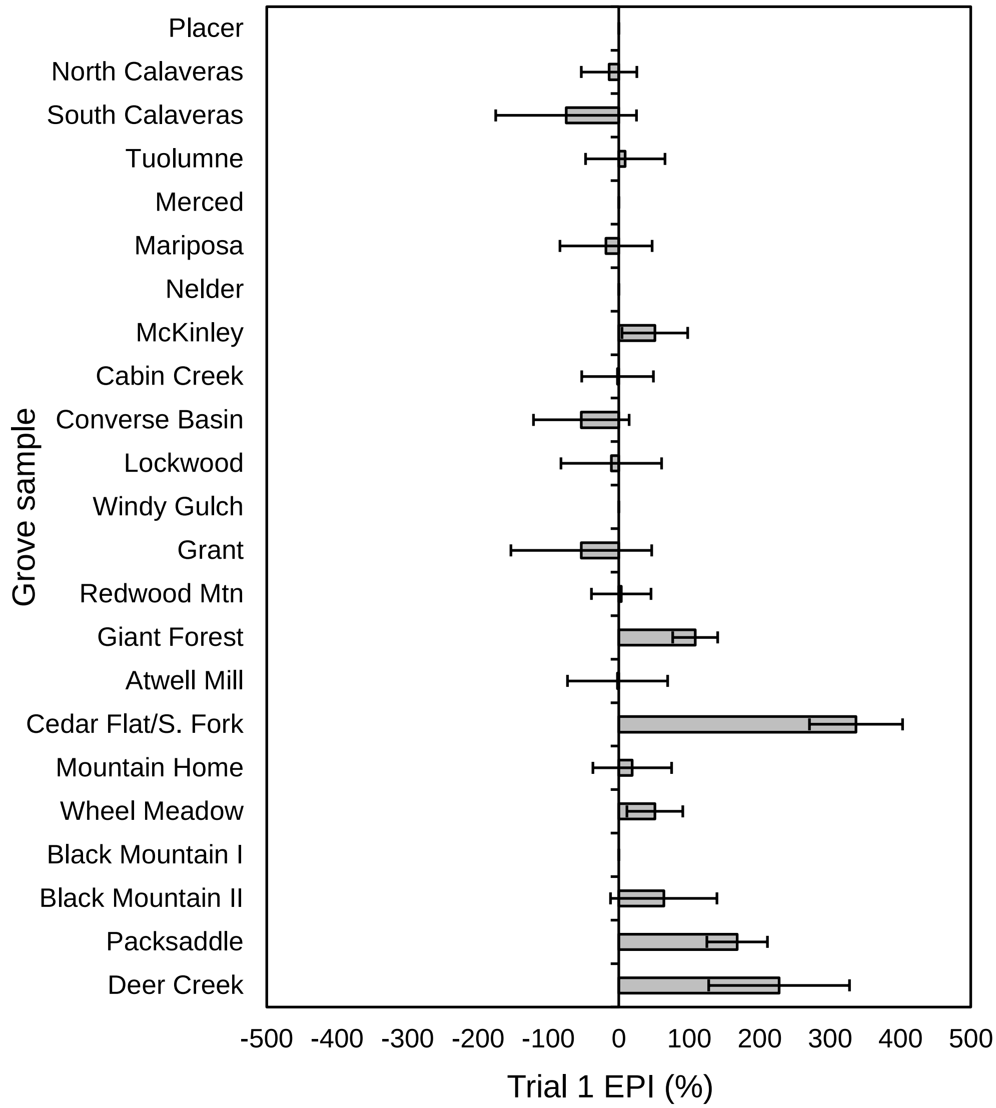


Figure 16. Trial 1 SEGI steckling grove sample epicormic sprouting abundance (EPI) in percent above or below the overall mean at Foresthill Seed Orchard after 29 growing seasons. There were no epicormic sprouts recorded for Placer, Merced, Nelder, Windy Gulch, or Black Mountain I grove samples. Among-grove differences were statistically significant ($p \leq 0.1$) in a Kruskal-Wallis test at alpha = 0.1. Error bars are relative standard errors of the grove sample mean, where the grove sample standard error is divided by the mean and expressed as a percent (%). Grove samples arranged from north to south in the figure.

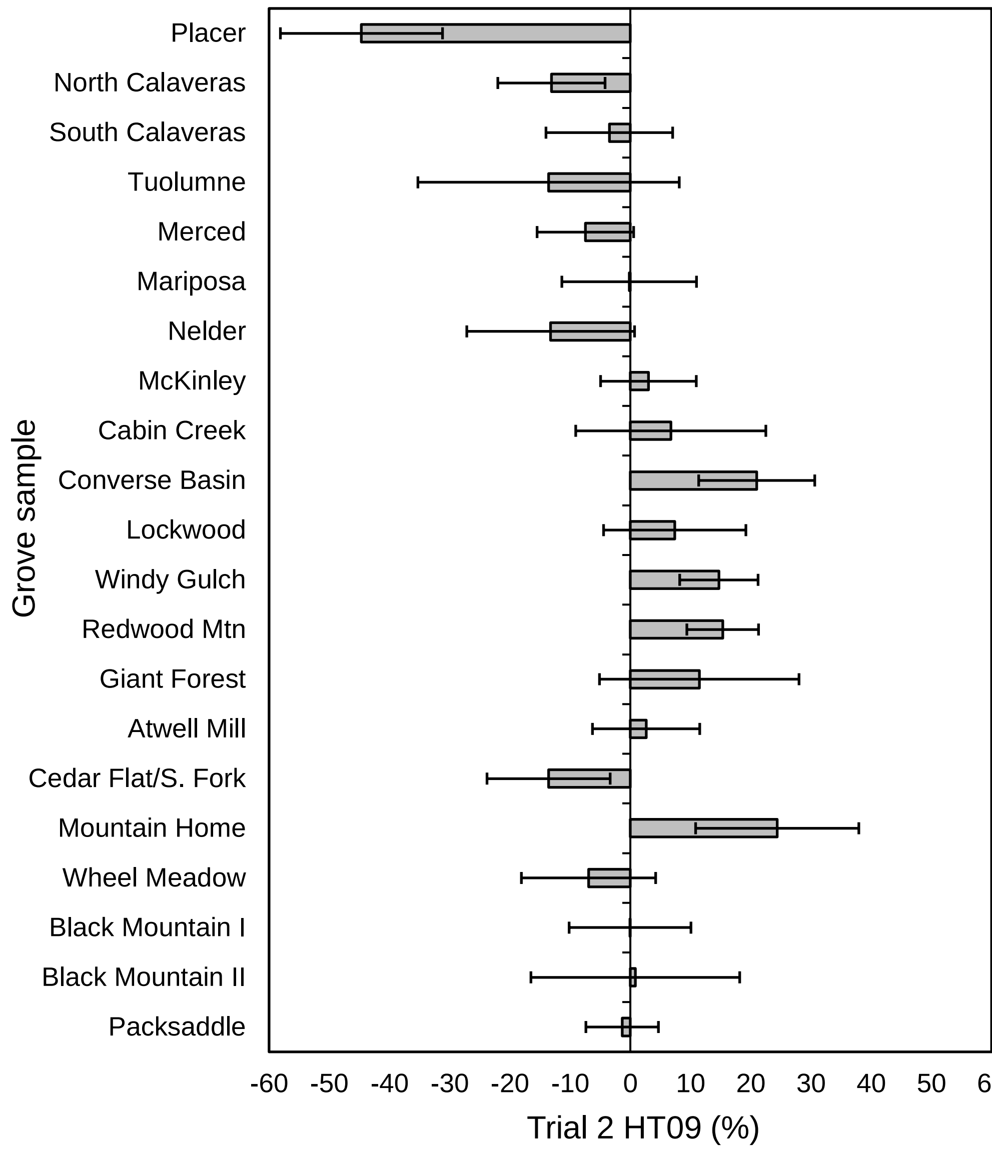


Figure 17. Trial 2 SEGI steckling grove sample mean height (HT09) in percent above or below the steckling mean after 29 growing seasons at Foresthill Seed Orchard as of 2009. Error bars are relative standard errors (%). Error bars are relative standard errors of the grove sample mean, where the grove sample standard error is divided by the mean and expressed as a percent (%). Grove samples arranged from north to south in the figure.

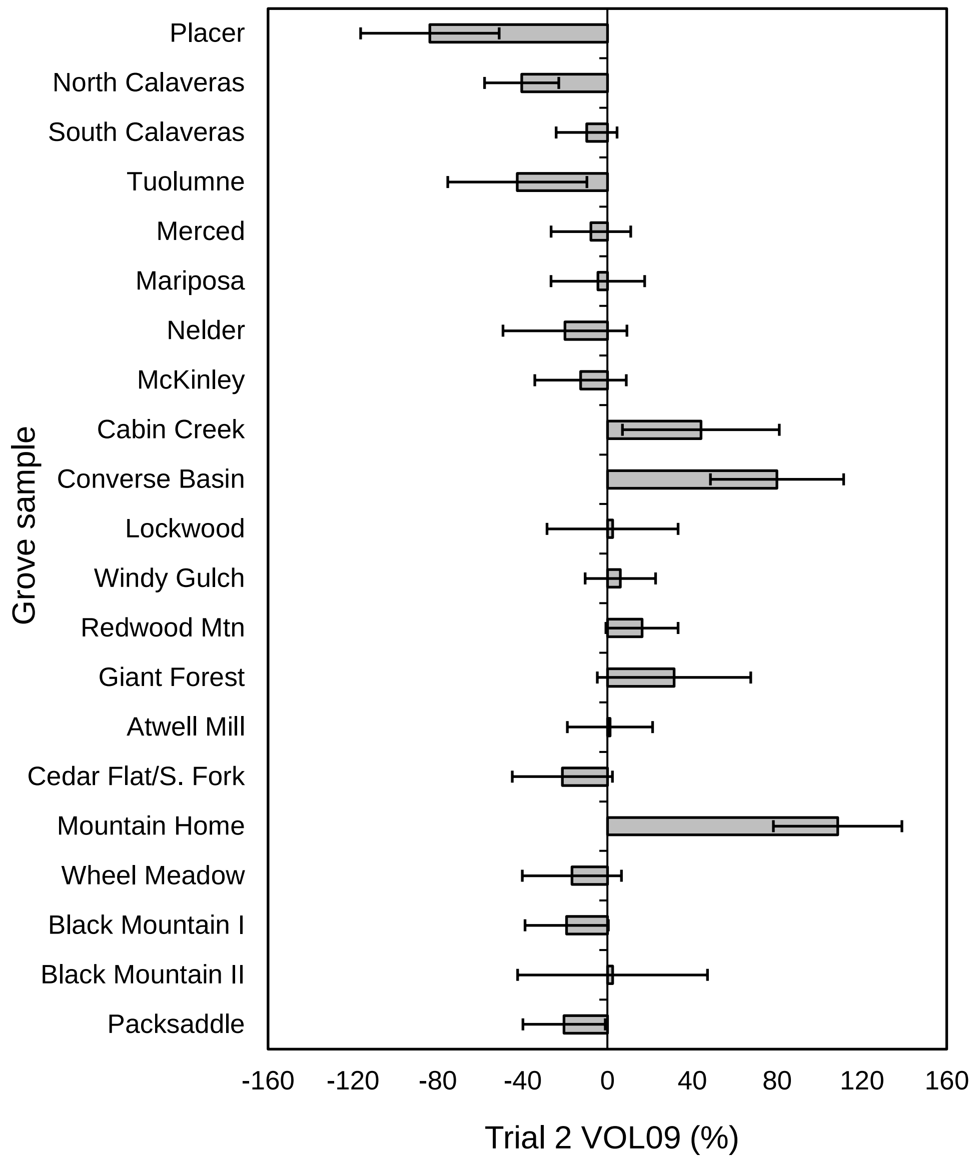


Figure 18. Trial 2 SEGI steckling grove sample mean conic stem volume (VOL09) in percent above or below the steckling mean after 29 growing seasons at Foresthill Seed Orchard as of 2009. Error bars are relative standard errors of the grove sample mean, where the grove sample standard error is divided by the mean and expressed as a percent (%). Grove samples arranged from north to south in the figure.

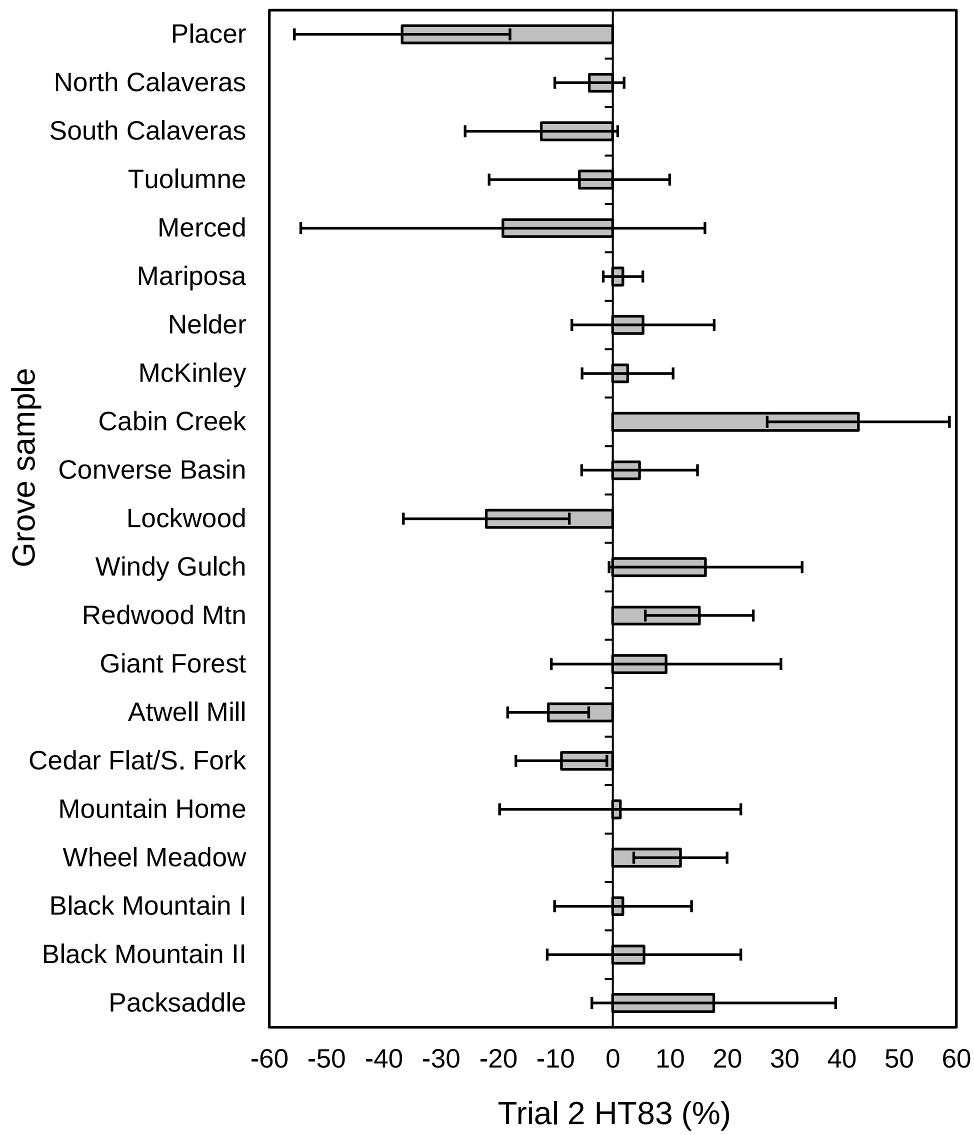


Figure 19. Trial 2 SEGI steckling grove sample mean height (HT83) in percent above or below the steckling mean after three growing seasons at Foresthill Seed Orchard as of 1983. Error bars are relative standard errors of the grove sample mean, where the grove sample standard error is divided by the mean and expressed as a percent (%). Grove samples arranged from north to south in the figure.

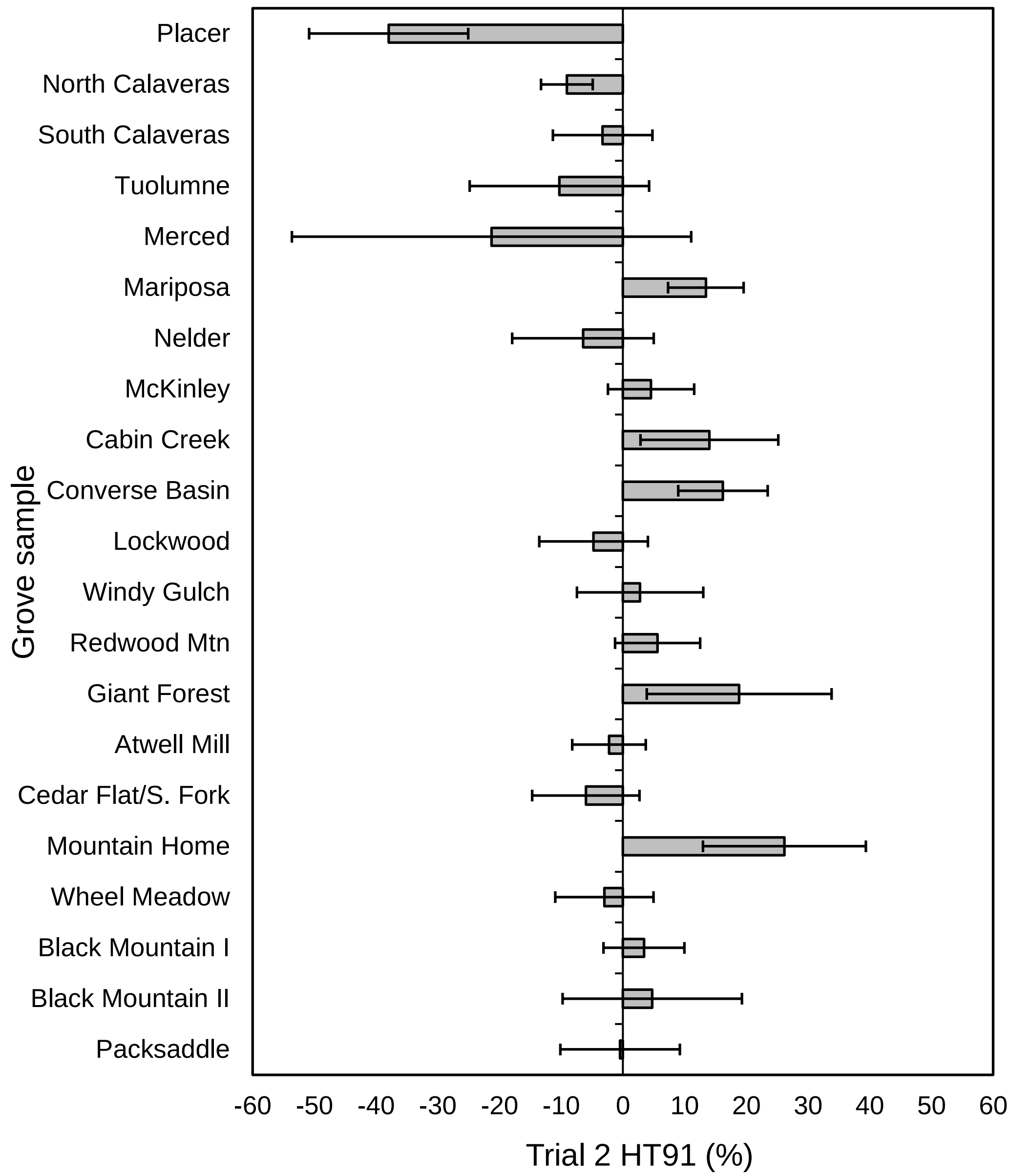


Figure 20. Trial 2 SEGI steckling grove sample mean height (HT91) in percent above or below the steckling mean after three growing seasons at Foresthill Seed Orchard as of 1991. Error bars are relative standard errors of the grove sample mean, where the grove sample standard error is divided by the mean and expressed as a percent (%). Grove samples arranged from north to south in the figure.

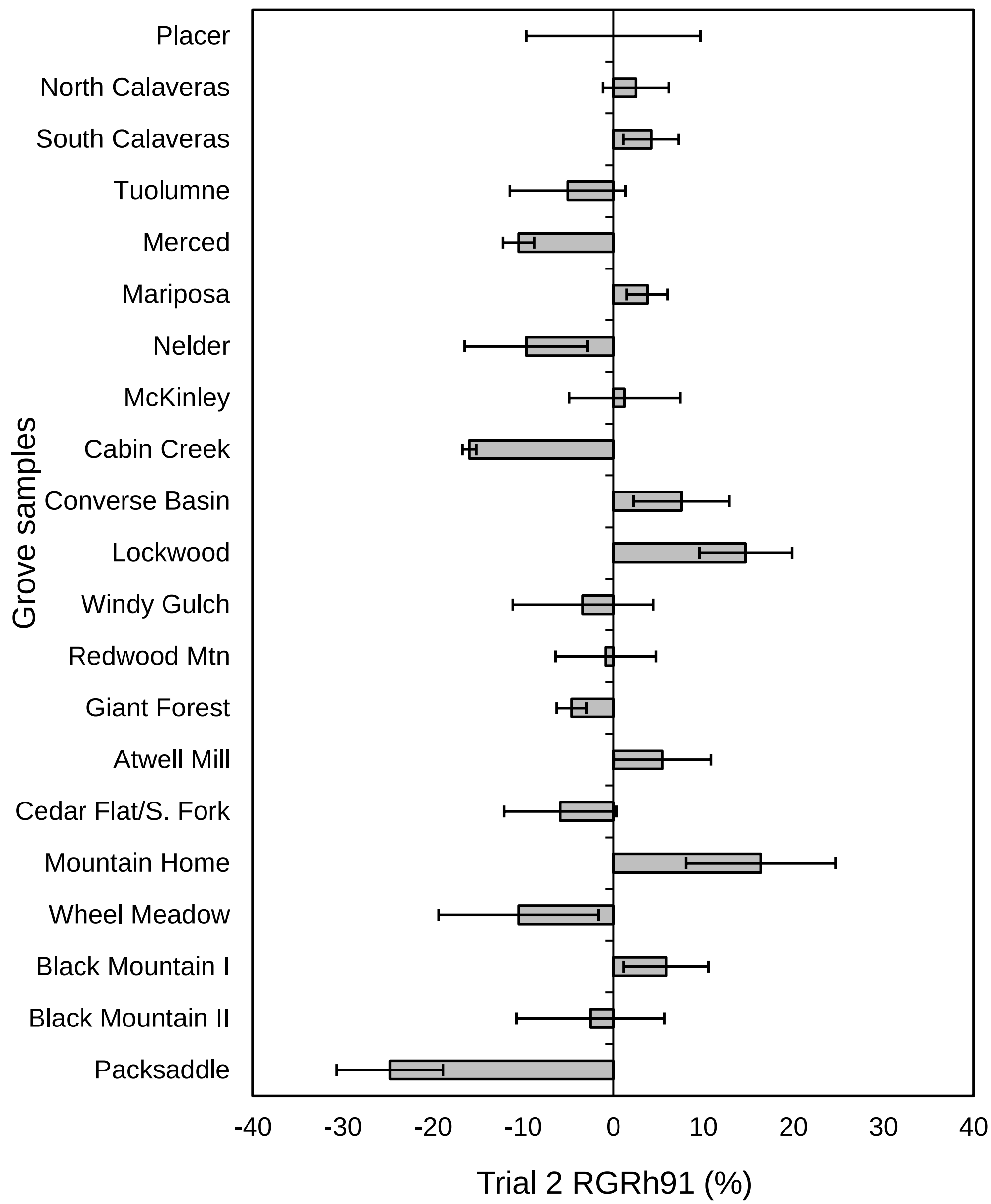


Figure 21. Trial 2 SEGI steckling grove sample mean relative height growth rate (RGRh91) over three growing seasons at Foresthill Seed Orchard from 1988 to 1991 in percent above or below the overall mean. Among-grove differences were statistically significant ($p \leq 0.05$) in a Kruskal-Wallis non-parametric test. Placer and Deer Creek grove samples were not included in analysis. Error bars are relative standard errors of the grove sample mean, where the grove sample standard error is divided by the mean and expressed as a percent (%). Grove samples arranged from north to south in the figure.

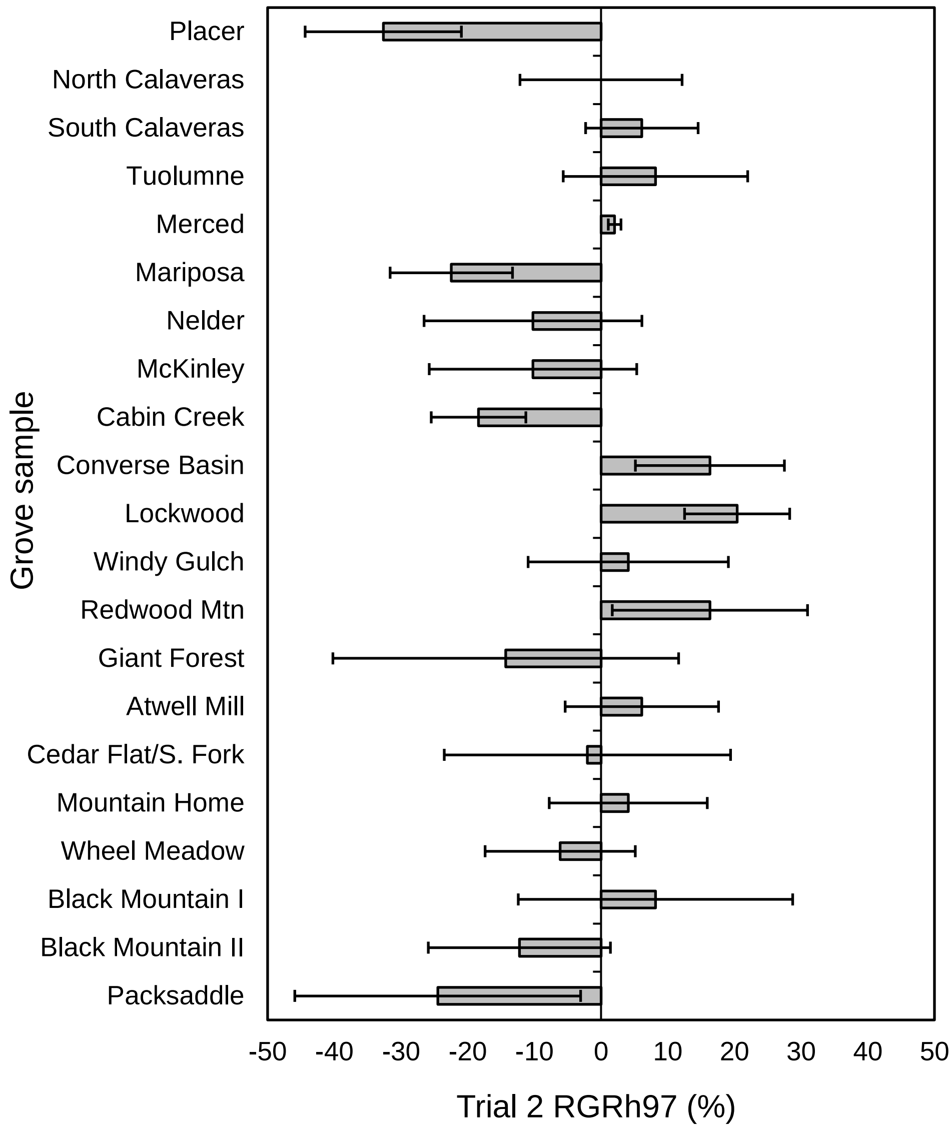


Figure 22. Trial 2 SEGI steckling grove sample mean relative height growth rate (RGRh97) over three growing seasons at Foresthill Seed Orchard from 1991 to 1997 in percent above or below the overall mean. Error bars are relative standard errors of the grove sample mean, where the grove sample standard error is divided by the mean and expressed as a percent (%). Grove samples arranged from north to south in the figure.

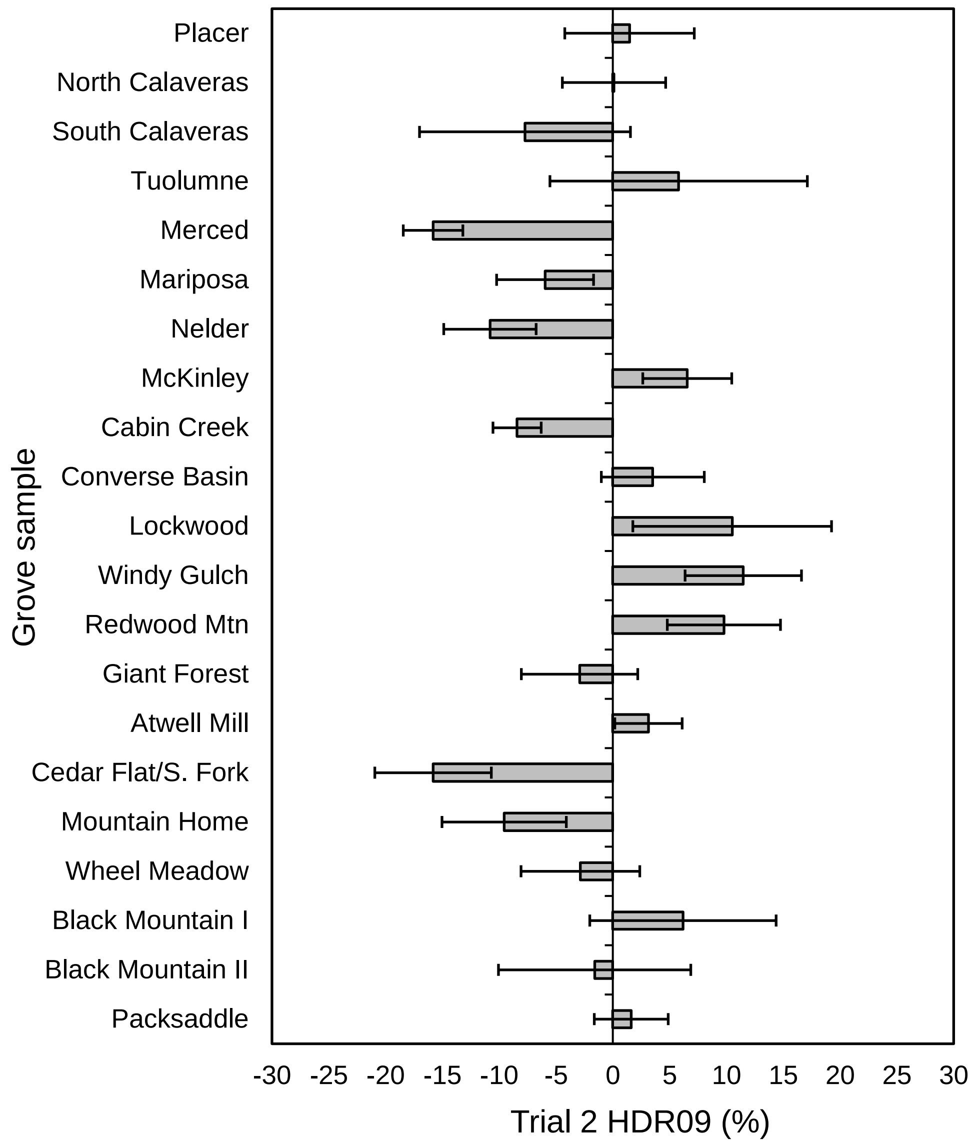


Figure 23. Trial 2 SEGI steckling grove sample mean height-diameter ratio (HDR09) in percent above or below the overall mean after 29 growing seasons at Foresthill Seed Orchard. Error bars are relative standard errors (%). Error bars are relative standard errors of the grove sample mean, where the grove sample standard error is divided by the mean and expressed as a percent (%). Grove samples arranged from north to south in the figure.

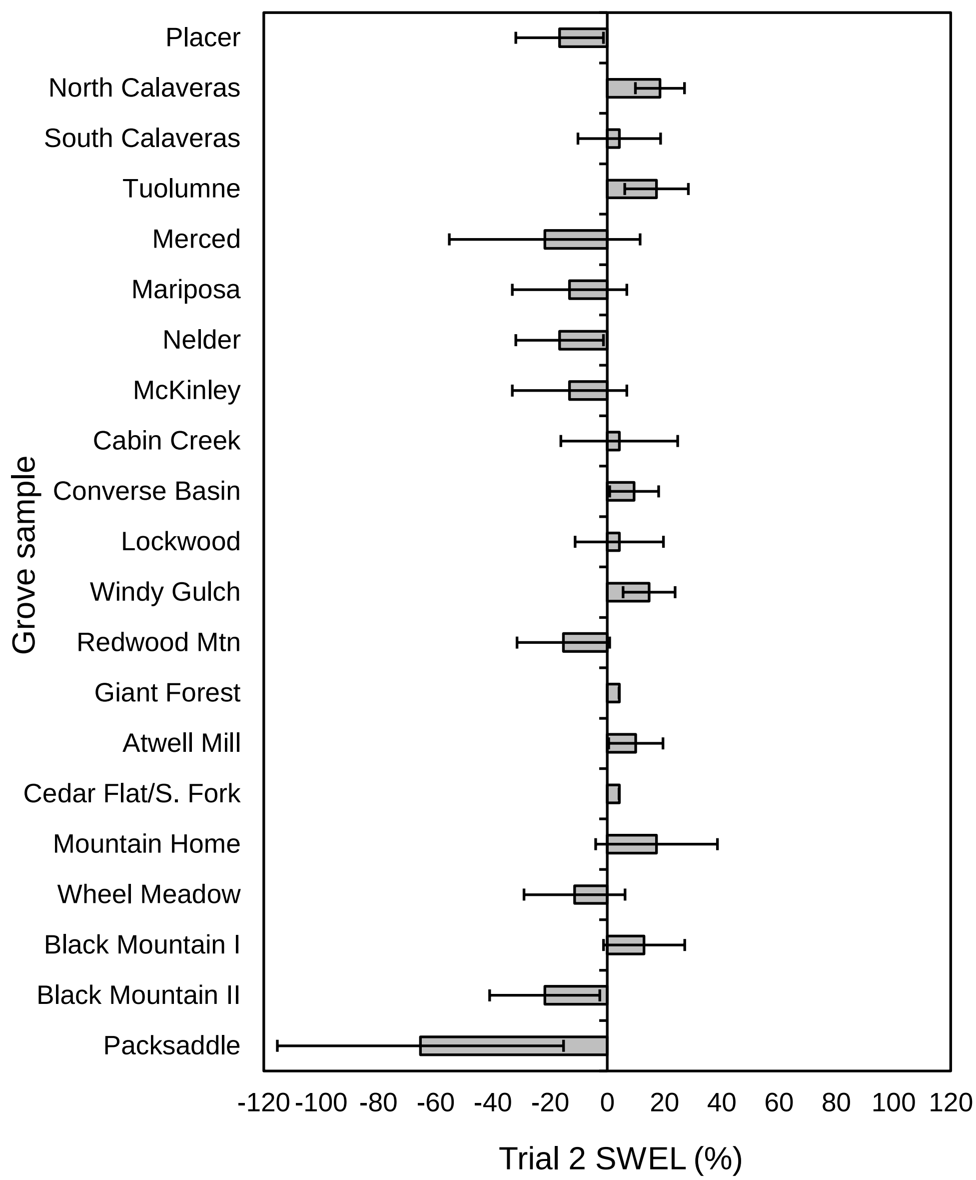


Figure 24. Trial 2 SEGI steckling grove sample mean basal swelling (SWEL) in percent above or below the within-trial steckling mean at Foresthill Seed Orchard. Error bars are relative standard errors of the grove sample mean, where the grove sample standard error is divided by the mean and expressed as a percent (%). Grove samples arranged from north to south in the figure.

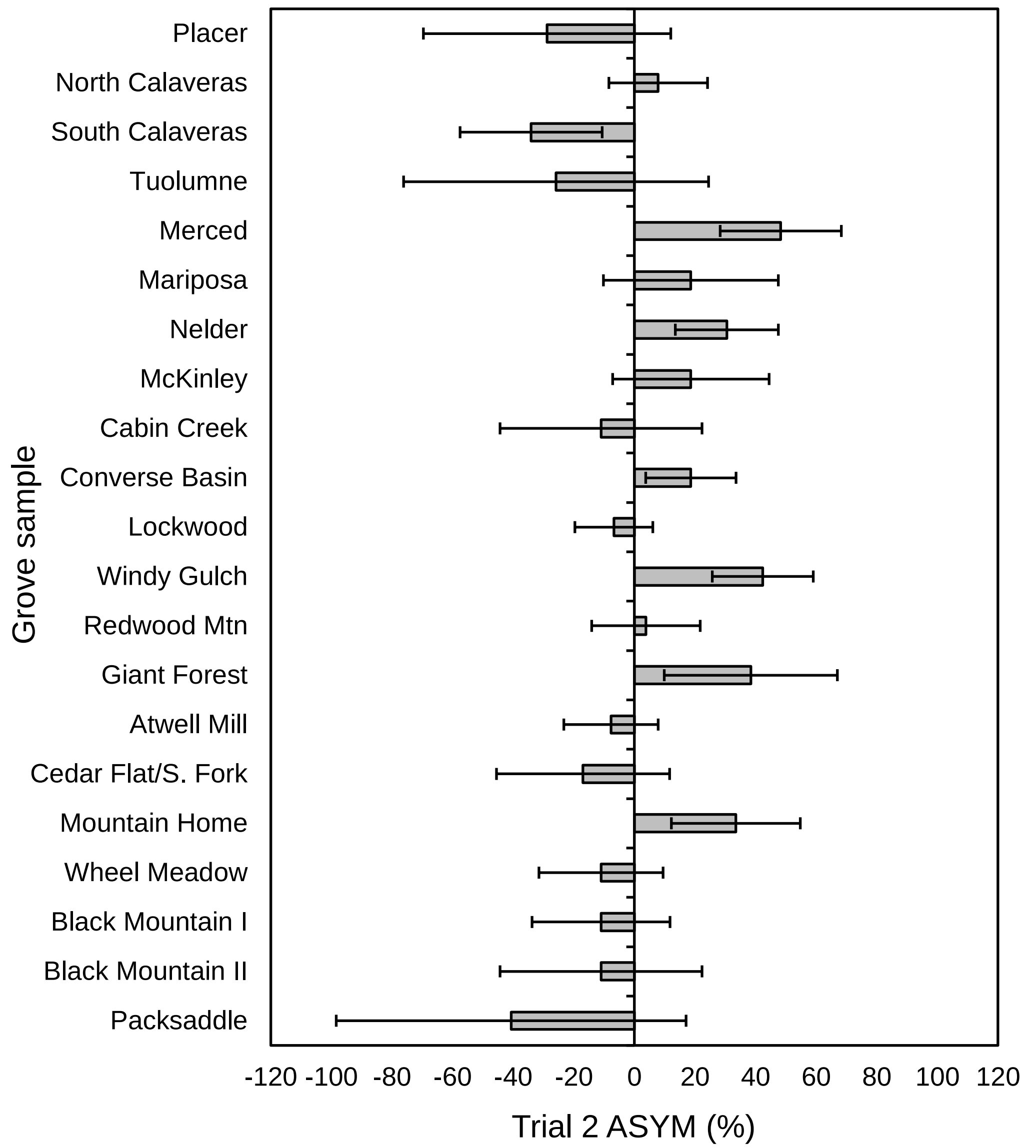


Figure 25. Trial 2 SEGI steckling grove sample mean lower stem asymmetry (ASYM) in percent above or below the within-trial steckling mean at Foresthill Seed Orchard. Error bars are relative standard errors of the grove sample mean, where the grove sample standard error is divided by the mean and expressed as a percent (%). Grove samples arranged from north to south in the figure.

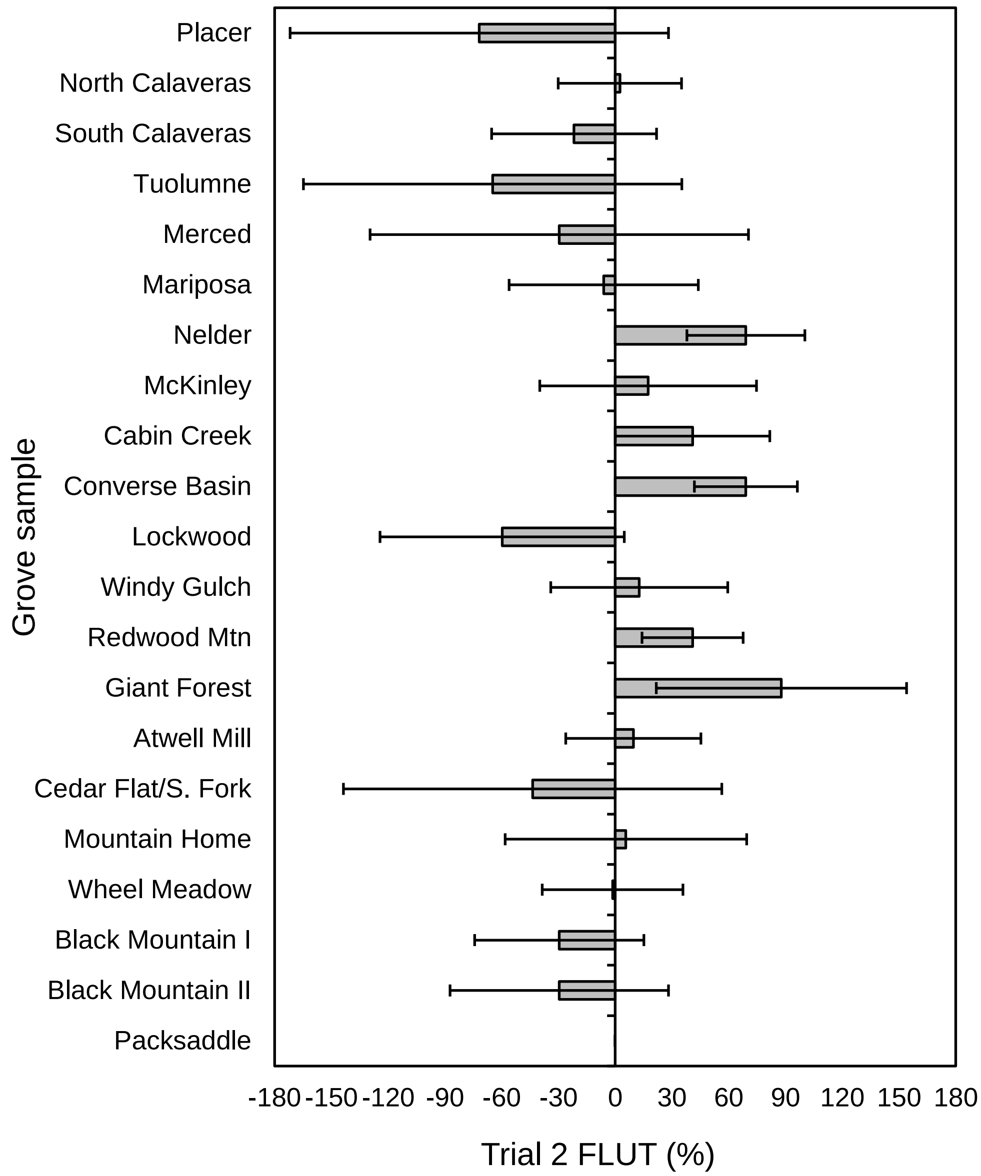


Figure 26. Trial 2 SEGI steckling grove sample mean lower stem fluting (FLUT) in percent above or below the within-trial steckling mean at Foresthill Seed Orchard. Packsaddle had no observed fluting. Error bars are relative standard errors of the grove sample mean, where the grove sample standard error is divided by the mean and expressed as a percent (%). Grove samples arranged from north to south in the figure.

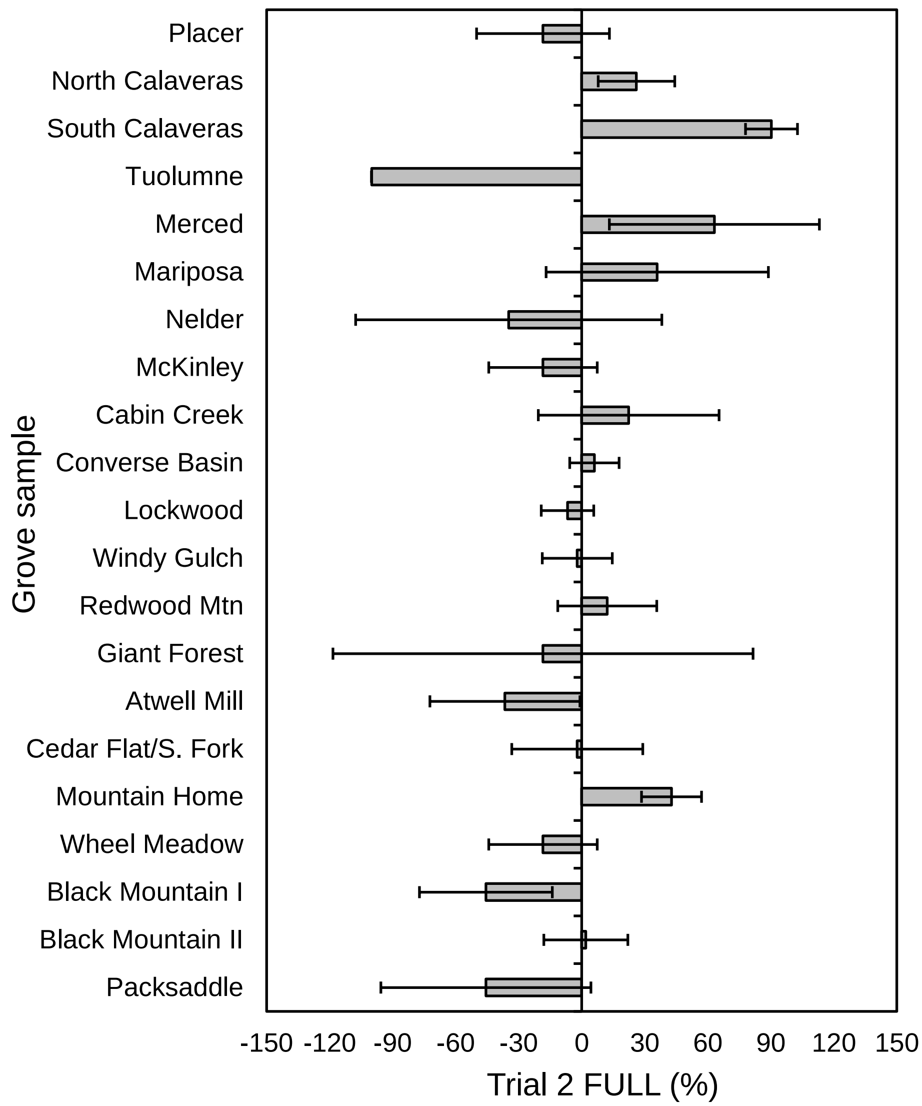


Figure 27. Trial 2 SEGI steckling grove sample mean crown fullness (FULL) in percent above or below the within-trial steckling mean at Foresthill Seed Orchard. Among-grove differences were statistically significant ($p \leq 0.05$) in a Kruskal-Wallis non-parametric test. Placer and Deer Creek grove samples were not included in analysis. Error bars are relative standard errors of the grove sample mean, where the grove sample standard error is divided by the mean and expressed as a percent (%). Grove samples arranged from north to south in the figure.

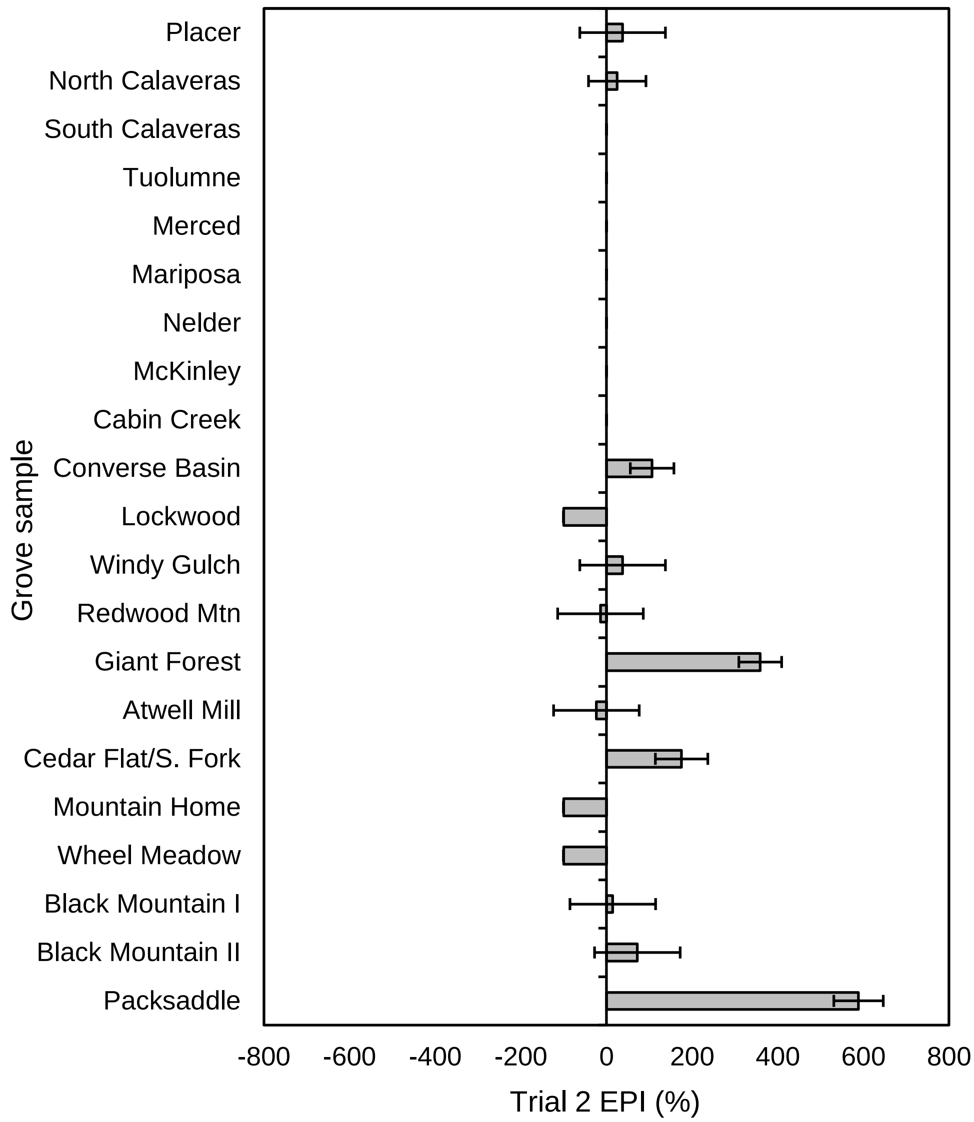


Figure 28. Trial 2 SEGI steckling grove sample mean epicormic sprout abundance (EPI) in percent above or below the within-trial steckling mean at Foresthill Seed Orchard. Among-grove differences were statistically significant ($p \leq 0.1$) in a Kruskal-Wallis test at alpha = 0.1. Error bars are relative standard errors of the grove sample mean, where the grove sample standard error is divided by the mean and expressed as a percent (%). Grove samples arranged from north to south in the figure.

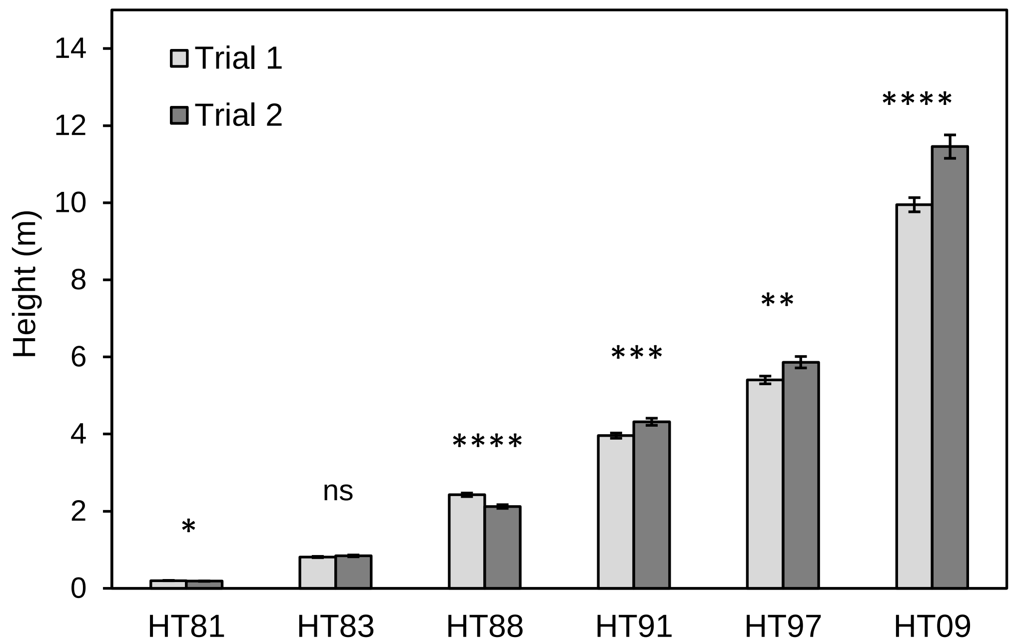


Figure 29. Mean height (HT) of SEGI stecklings in trial 1 (n = 235) and trial 2 (n = 124) in six measurement years over 29 growing seasons at Foresthill Seed Orchard Tests of significance were conducted using the non-parametric Kruskal-Wallis test. Trial 1 mean HT81 was significantly greater than trial 2. Levels of significance for each growth period indicated by asterisks (ns = no significance, * p < 0.05; ** p <0.001; ***p < 0.001; **** p < 0.0001).

Figure 30. Mean relative height growth rate (RGRh) of stecklings in trial 1 and trial 2 for five growth periods over 29 growing seasons at Foresthill Seed Orchard. Tests of significance were conducted using the non-parametric Kruskal-Wallis test. Trial 2 mean RGRh 1997-2009 was greater than trial 1. Levels of significance for each growth period indicated by asterisks (ns = no significance; * $p \leq 0.05$; ** $p \leq 0.01$; *** $p \leq 0.001$; **** $p \leq 0.0001$).

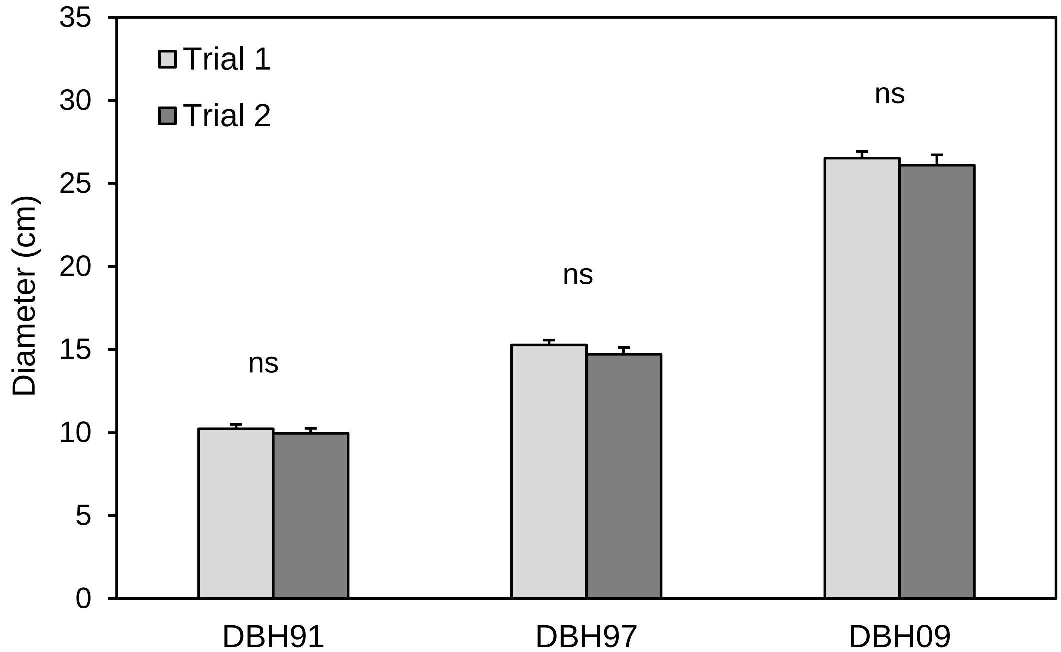


Figure 31. Mean diameter breast height (DBH) of SEGI stecklings in trial 1 and trial 2 in three measurement years over 29 growing seasons at Foresthill Seed Orchard. Tests of significance were conducted using the non-parametric Kruskal-Wallis test. Levels of significance for each growth period indicated by asterisks (ns = no significance; * $p < 0.05$; ** $p < 0.01$; *** $p < 0.001$; **** $p < 0.0001$).

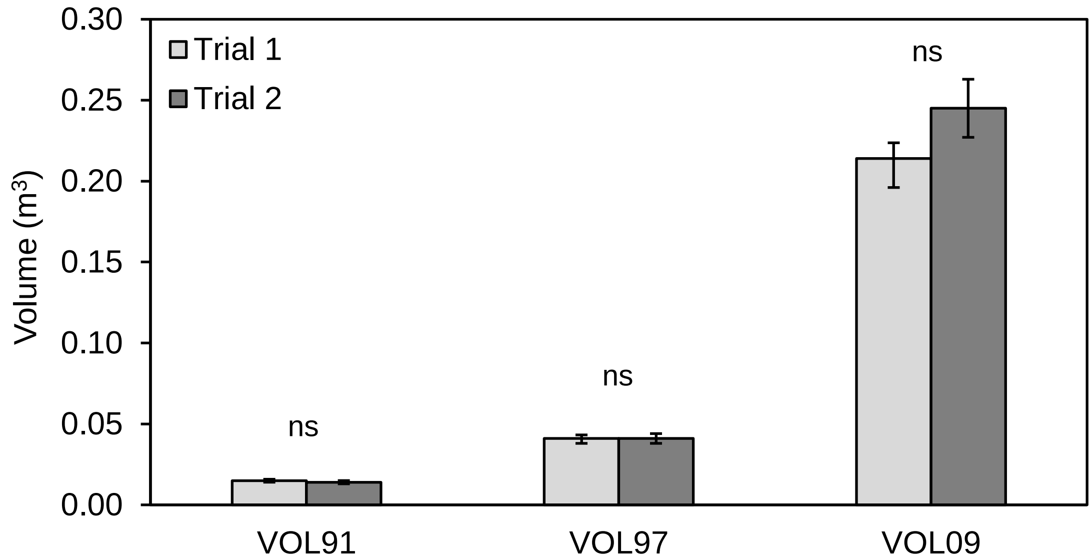


Figure 32. Mean conic stem volume (VOL) in SEGI stecklings in trial 1 and trial 2 in three measurement years over 29 growing seasons at Foresthill Seed Orchard. Tests of significance were conducted using the non-parametric Kruskal-Wallis test. Levels of significance for each growth period indicated by asterisks (ns = no significance; * $p < 0.05$; ** $p < 0.01$; *** $p < 0.001$; **** $p < 0.0001$).

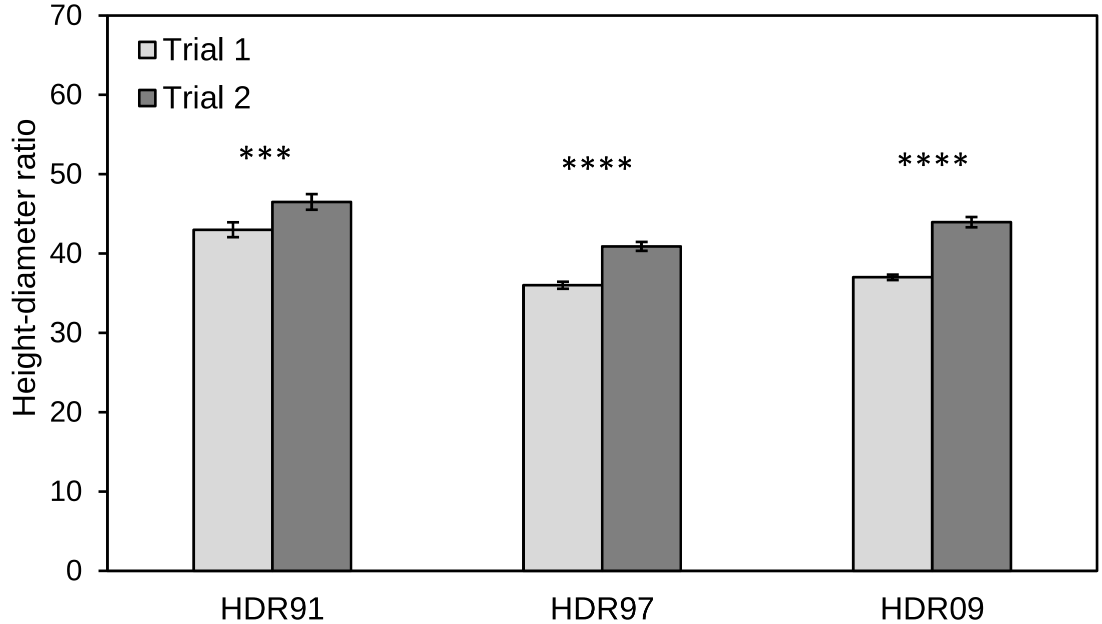


Figure 33. Mean height-diameter ratio (HDR) of SEGI stecklings in trial 1 and trial 2 in three measurement years over 29 growing seasons at Foresthill Seed Orchard. Tests of significance were conducted using the non-parametric Kruskal-Wallis test. Levels of significance for each growth period indicated by asterisks (ns = no significance; * $p < 0.05$; ** $p < 0.01$; ***$p < 0.001$; **** $p < 0.0001$).

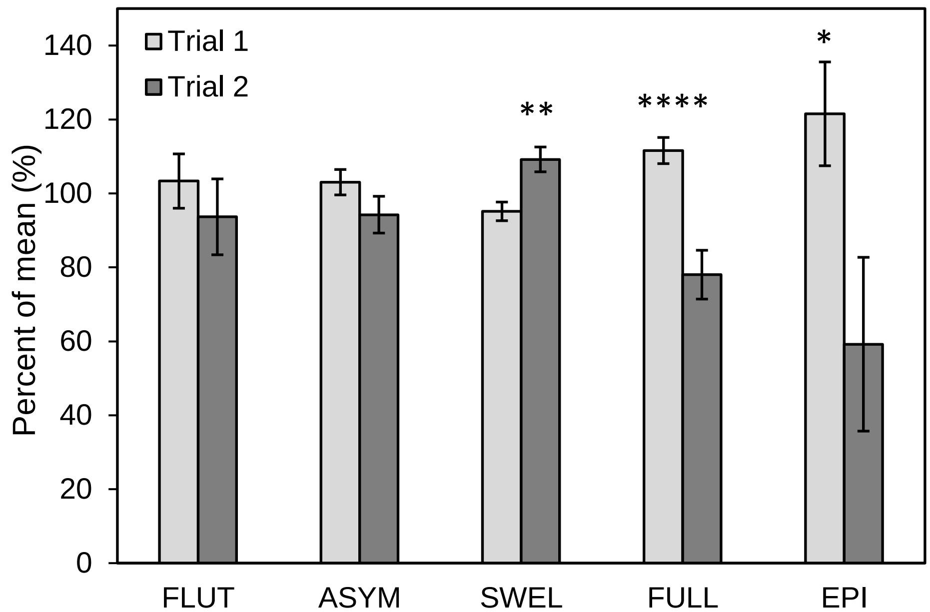
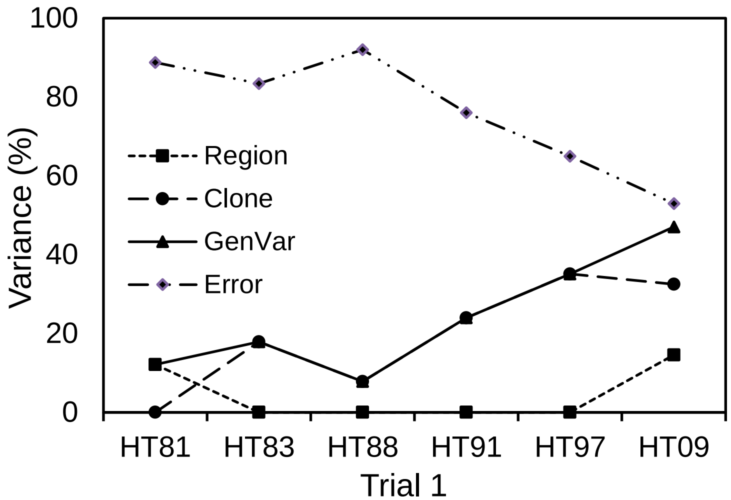


Figure 34. Comparison of trial 1 (n = 235) and trial 2 (n = 124) SEGI steckling form traits in percent of mean after 29 growing seasons at Foresthill Seed Orchard. Tests of significance were conducted using the non-parametric Kruskal-Wallis test. Error bars are relative standard errors of the trial mean where the trial standard error is divided by the mean and expressed as a percent. Levels of significance for each growth period indicated by asterisks (* $p < 0.05$; ** $p < 0.01$; *** $p < 0.001$; **** $p < 0.0001$).



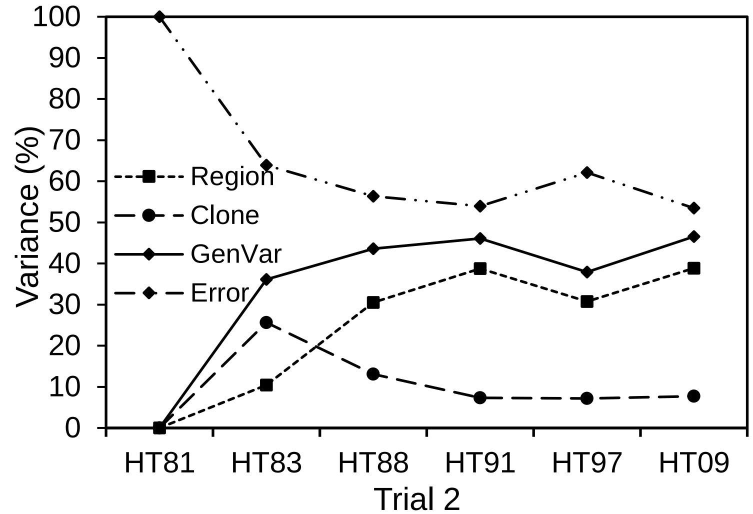


Figure 35. Phenotypic variance in tree height (HT) of trial 1 and trial 2 SEGI clone subset data partitioned into among-region (Region), among-clone within region (Clone), and environmental/error (Error) sources of variation in percent of variance in six measurement years from 1981 to 2009 at Foresthill Seed Orchard. Genetic variance (GenVar) is the sum of among-region and among-clone variances.

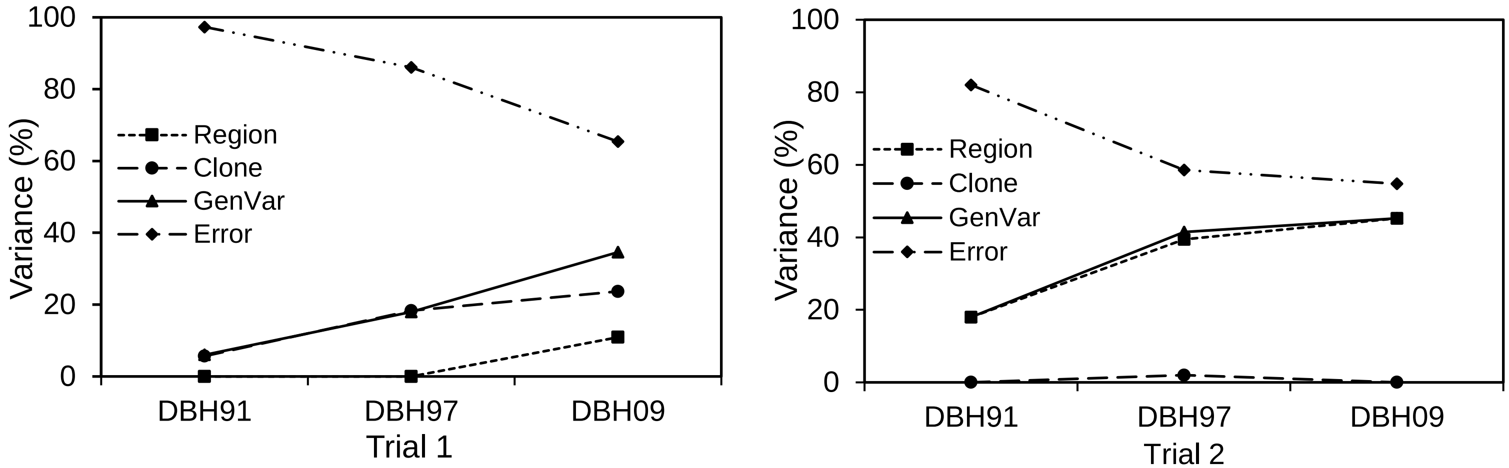


Figure 36. Phenotypic variance in stem diameter (DBH) of trial 1 and trial 2 SEGI clone subset data partitioned into among-region (Region), among-clone within region (Clone), and environmental/error (Error) sources of variation in percent of variance in three measurement years from 1991 to 2009 at Foresthill. Genetic variance (GenVar) is the sum of among-region and among-clone variances.

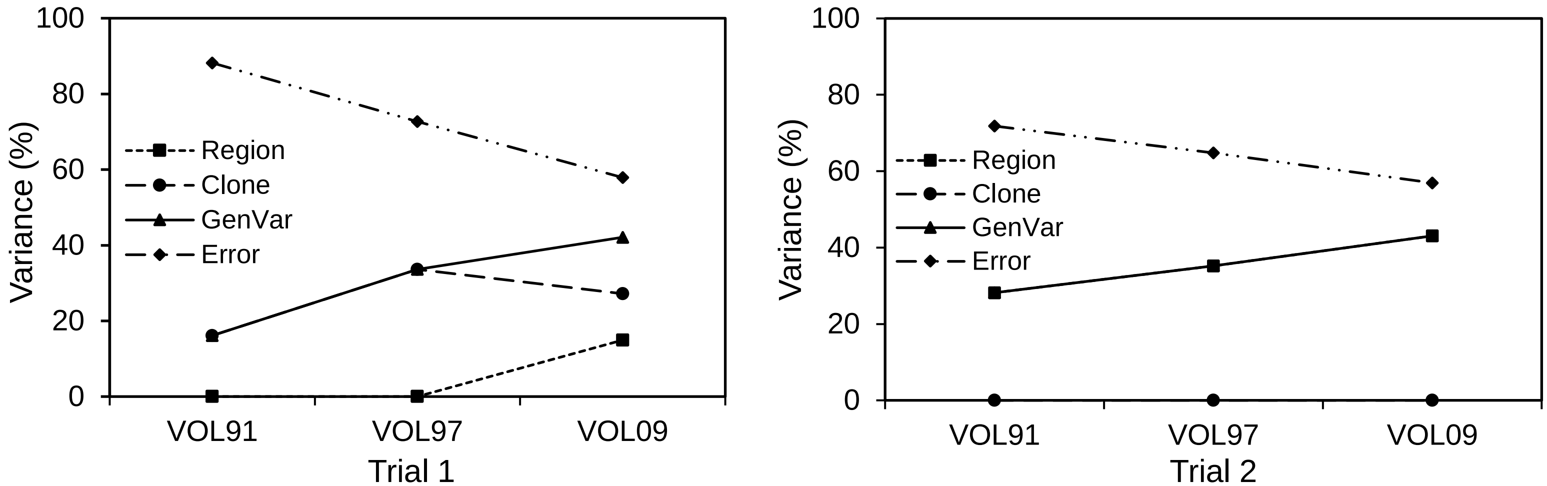


Figure 37. Phenotypic variance in stem-volume (VOL) of trial 1 and trial 2 SEGI clone subset data partitioned into among-region (Region), among-clone within region (Clone), and environmental/error (Error) sources of variation in percent of variance in three measurement years from 1991 to 2009 at Foresthill Seed Orchard. Genetic variance (GenVar) is the sum of among-region and among-clone variances.

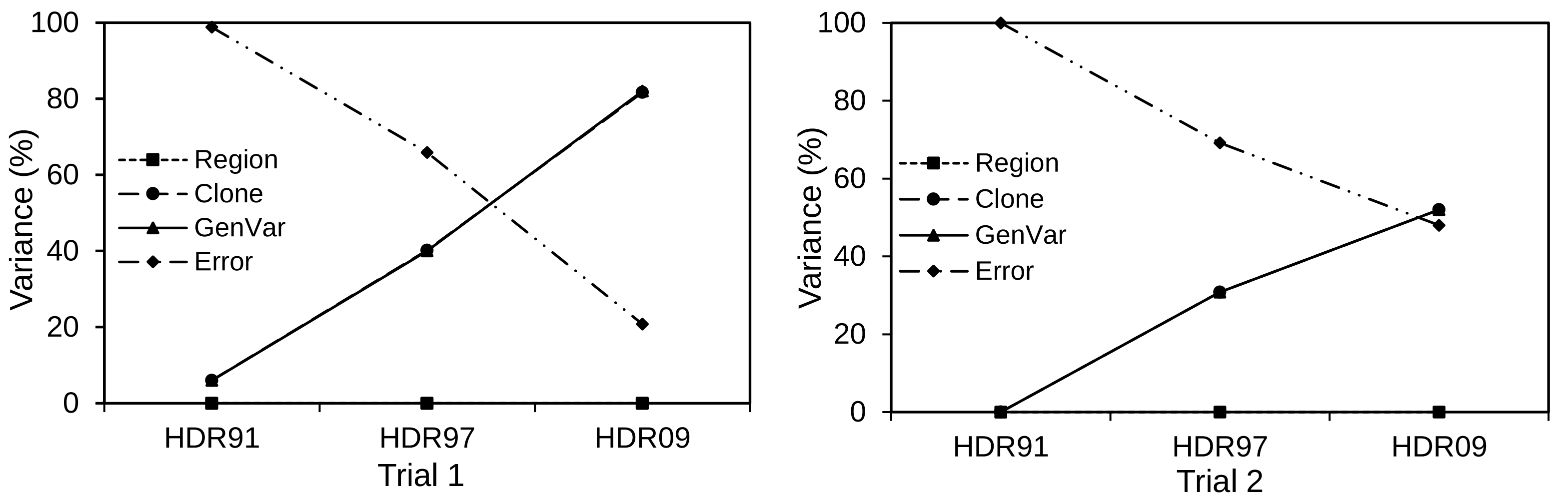


Figure 38. Phenotypic variance in height-diameter ratio (VOL) of trial 1 and trial 2 SEGI clone subset data partitioned into among-region (Region), among-clone within region (Clone), and environmental/error (Error) sources of variation in percent of variance in three measurement years from 1991 to 2009 at Foresthill Seed Orchard. Genetic variance (GenVar) was the sum of among-region and among-clone variances.

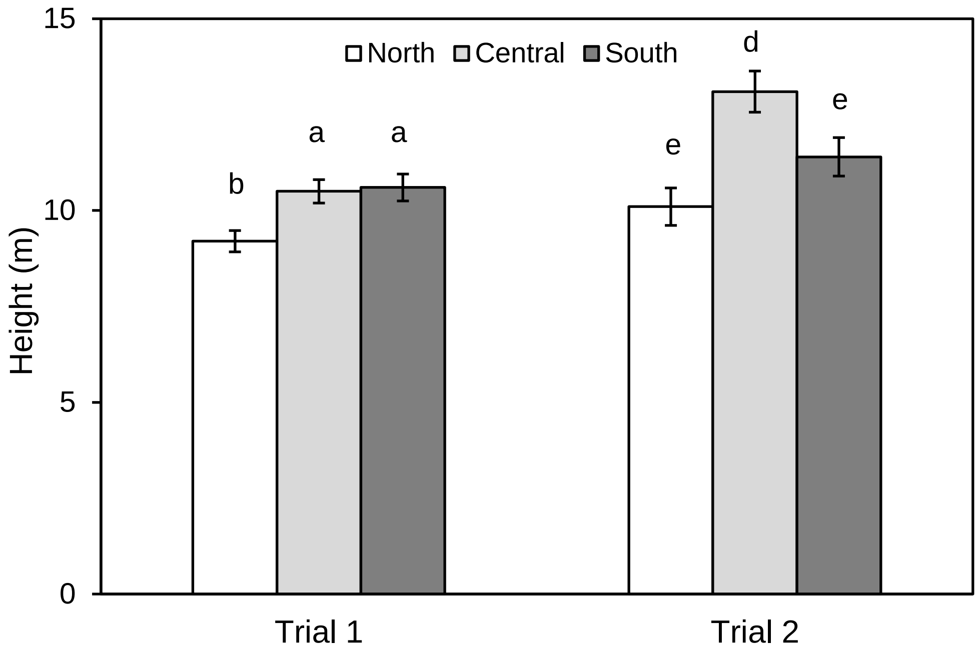


Figure 39. Mean height of SEGI stecklings in trial 1 and trial 2 by region of grove sample origin in the SEGI native range after 29 growing seasons at Foresthill Seed Orchard in 2009. Region of grove sample origin was statistically significant in trial 1 ($p \leq 0.01$) and trial 2 ($p \leq 0.01$). Multiple comparison tests conducted using Tukey-Kramer method. Letters indicate significant differences among groups within trials at $\alpha = 0.05$.

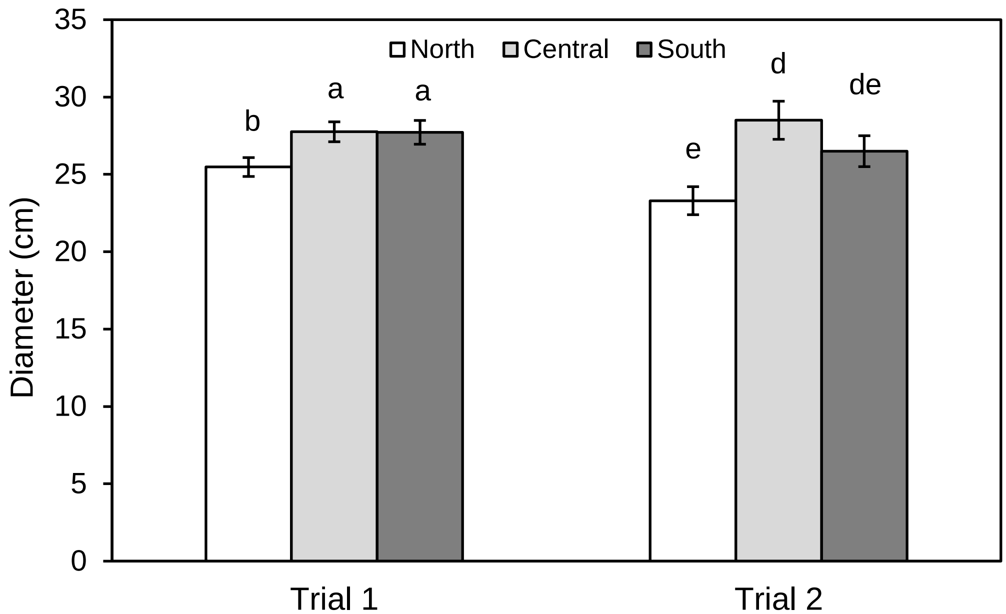


Figure 40. Mean stem diameter at breast height (DBH) of SEGI stecklings in trial 1 and trial 2 by region of grove sample origin in the SEGI native range after 29 growing seasons at Foresthill Seed Orchard in 2009. Region of grove sample origin was statistically significant in trial 1 ($p \leq 0.05$) and trial 2 ($p \leq 0.05$). Multiple comparison tests conducted using Tukey-Kramer method. Letters indicate significant differences among groups within trials at $\alpha = 0.05$.

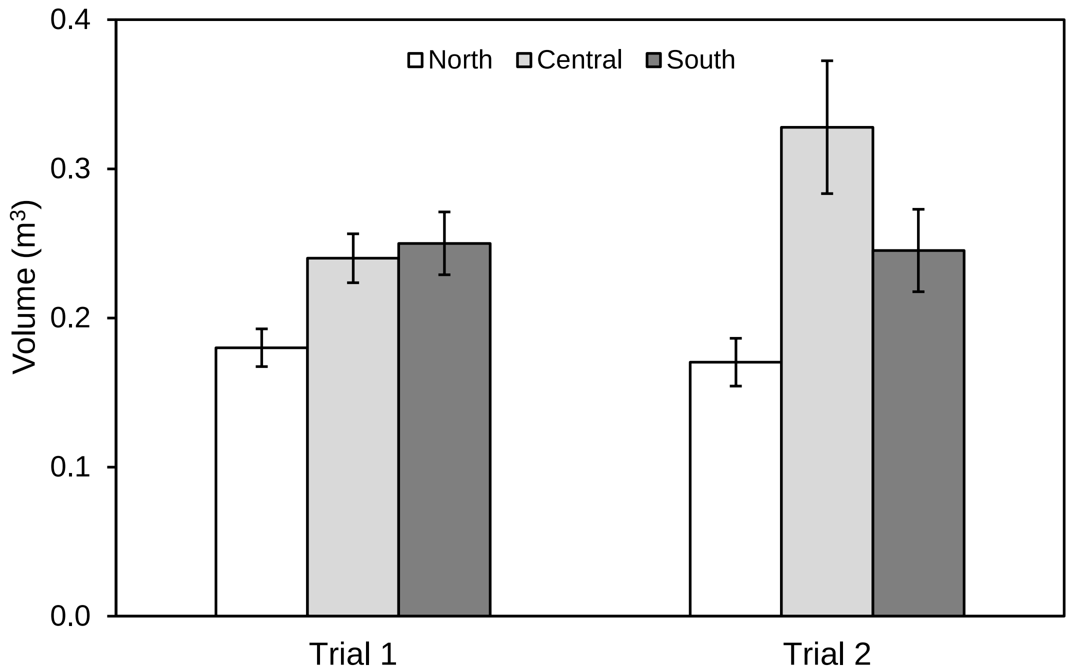


Figure 41. Mean stem volume (VOL) of SEGI stecklings in trial 1 and trial 2 by region of grove sample origin in the SEGI native range after 29 growing seasons at Foresthill Seed Orchard in 2009. In non-parametric Kruskal-Wallis test, region of grove sample origin was statistically significant in trial 1 ($p \leq 0.001$) and trial 2 ($p \leq 0.05$) No multiple comparison significance tests were conducted.

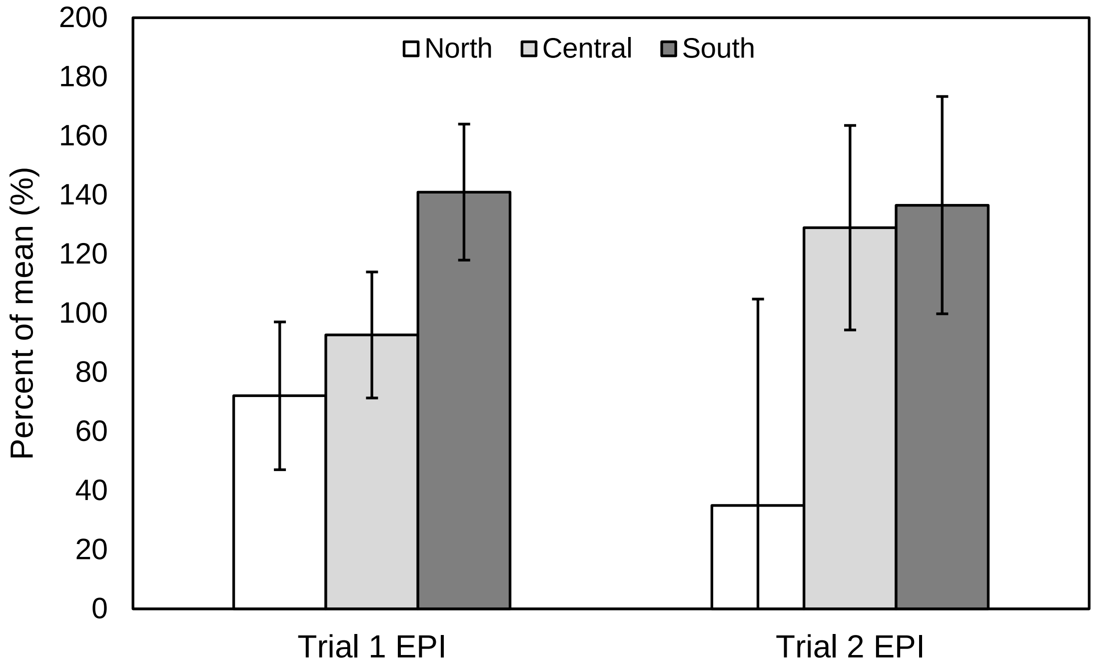


Figure 42. Percent of mean epicormic sprouting (EPI) of SEGI stecklings in trial 1 and trial 2 by region of grove sample origin in the SEGI native range after 29 growing seasons at Foresthill Seed Orchard in 2009.

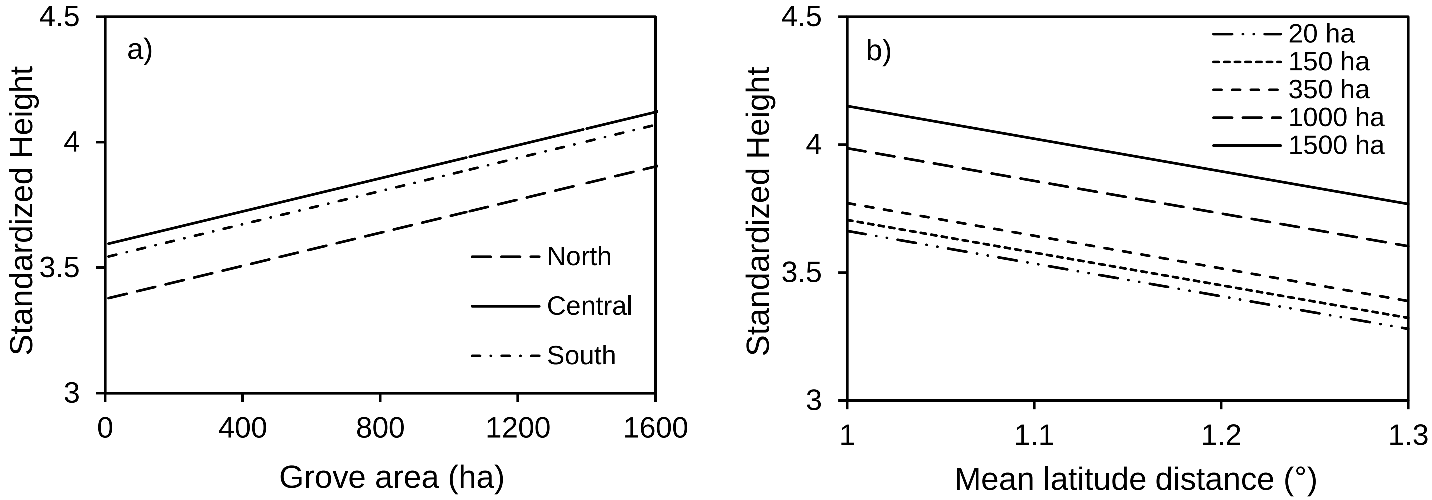


Figure 43. Model simulation of the best model of SEGI steckling standardized height 2009 as a function of native grove geographic characteristics for range-wide steckling grove samples from trial 1 and 2. The effects of the best predictor variables a) grove area (ha) by region of native grove origin and b) mean distance of grove sample to two nearest two neighboring sampled native groves in degrees latitude plus one (0° = 1°) for five grove area categories.

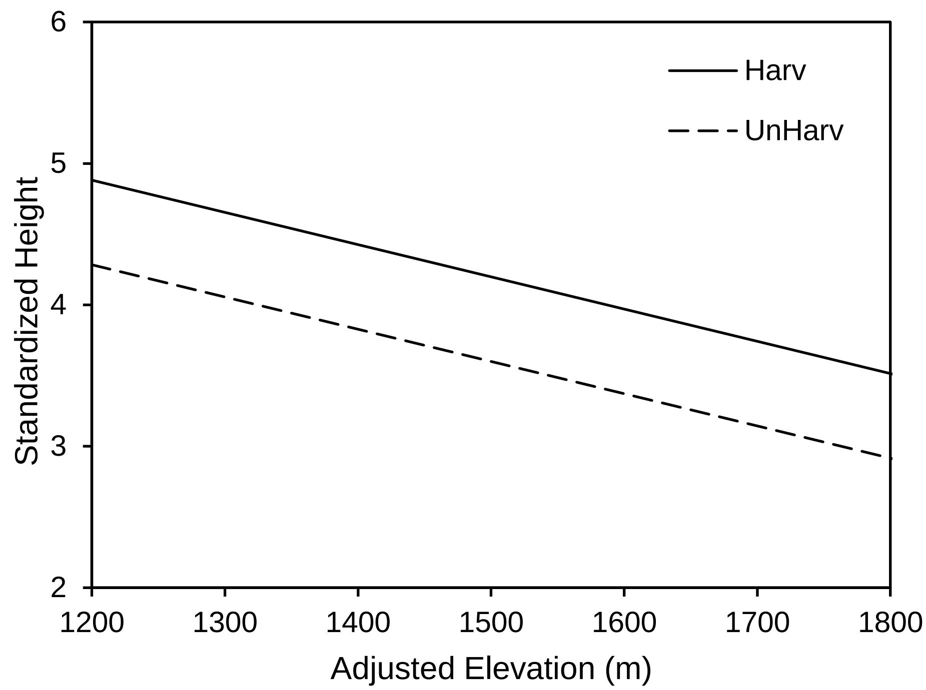


Figure 44. Model simulation of the best model of SEGI steckling standardized height in 2009 as a function of native grove geographic characteristics for SEGI steckling grove samples from trial 1 and 2 originating from large- and very large-sized native grove areas.. The effect of the best predictor variables adjusted elevation and harvest history are shown for harvested groves (Harv) and unharvested groves (UnHarv).

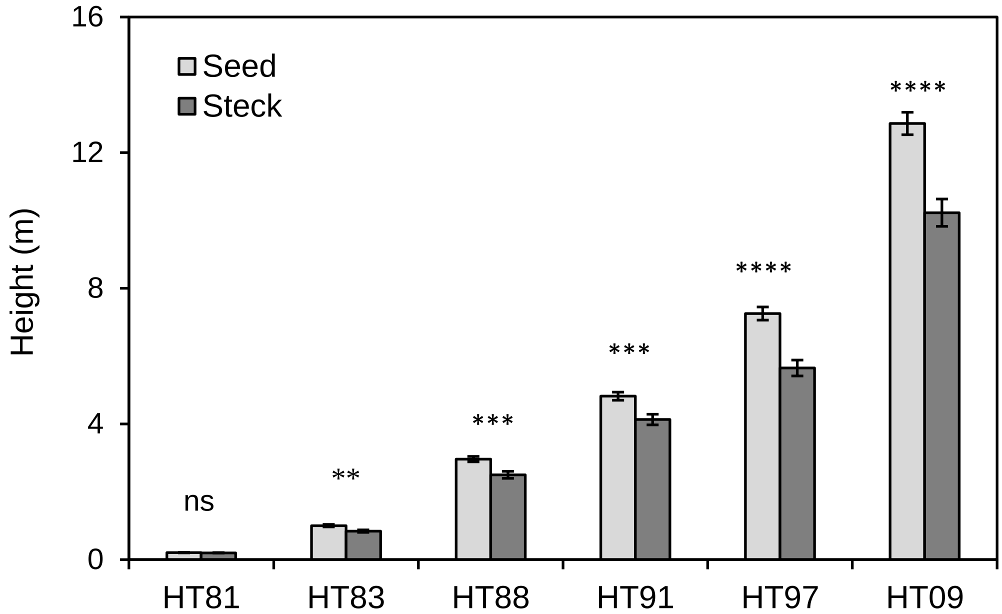


Figure 45. Trial 1 seedling (Seed; n = 68) and steckling (Steck; n = 63) height in six measurement years over 29 growing seasons at Foresthill Seed Orchard. Only grove samples with both seedlings and stecklings planted in trial 1 were included in this analysis. Tests of significance were conducted using the non-parametric Kruskal-Wallis test. Levels of significance for each growth period indicated by asterisks (ns = no significance; * $p < 0.05$; ** $p < 0.01$; ***$p < 0.001$; **** $p < 0.0001$).

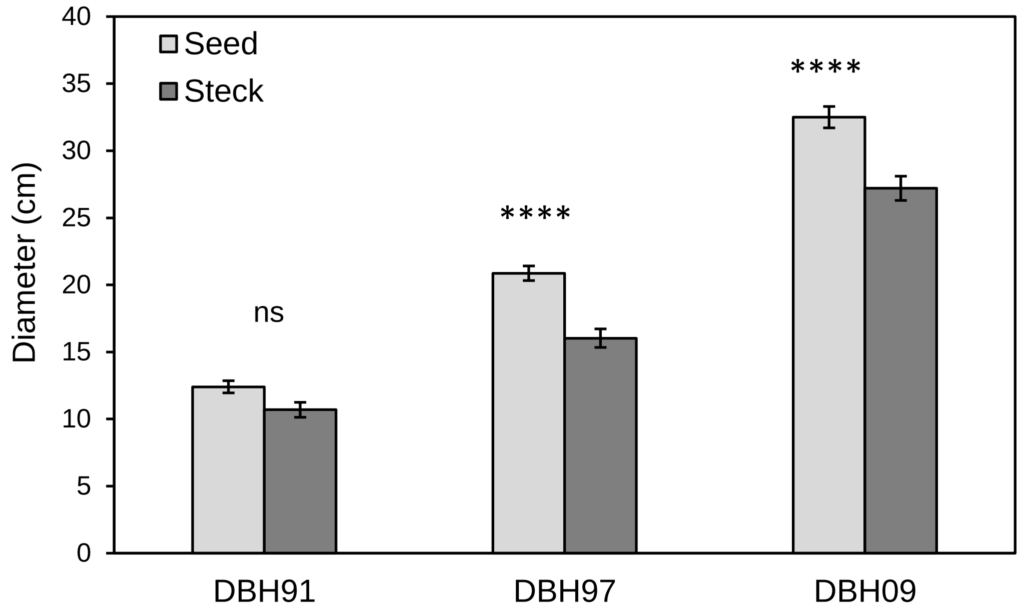


Figure 46. Trial 1 seedling (Seed; n = 68) and steckling (Steck; n = 63) stem diameter in six measurement years over 29 growing seasons at Foresthill Seed Orchard. Only grove samples with both seedlings and stecklings planted in trial 1 were included in this analysis. Tests of significance were conducted using the non-parametric Kruskal-Wallis test. Levels of significance for each growth period indicated by asterisks (ns = no significance; * $p < 0.05$; ** $p < 0.01$; ***$p < 0.001$; **** $p < 0.0001$).

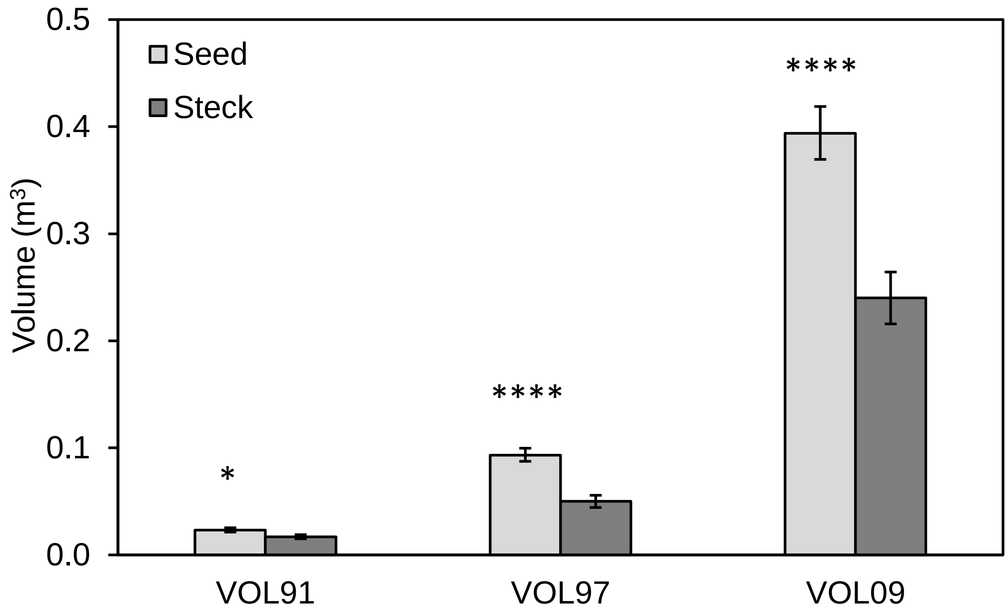


Figure 47. Trial 1 seedling (Seed; n = 68) and steckling (Steck; n = 63) conic stem volume in six measurement years over 29 growing seasons at Foresthill Seed Orchard. Only grove samples with both seedlings and stecklings planted in trial 1 were included in this analysis. Tests of significance were conducted using the non-parametric Kruskal-Wallis test. Levels of significance for each growth period indicated by asterisks (ns = no significance; * $p < 0.05$; ** $p < 0.01$; ***$p < 0.001$; **** $p < 0.0001$).

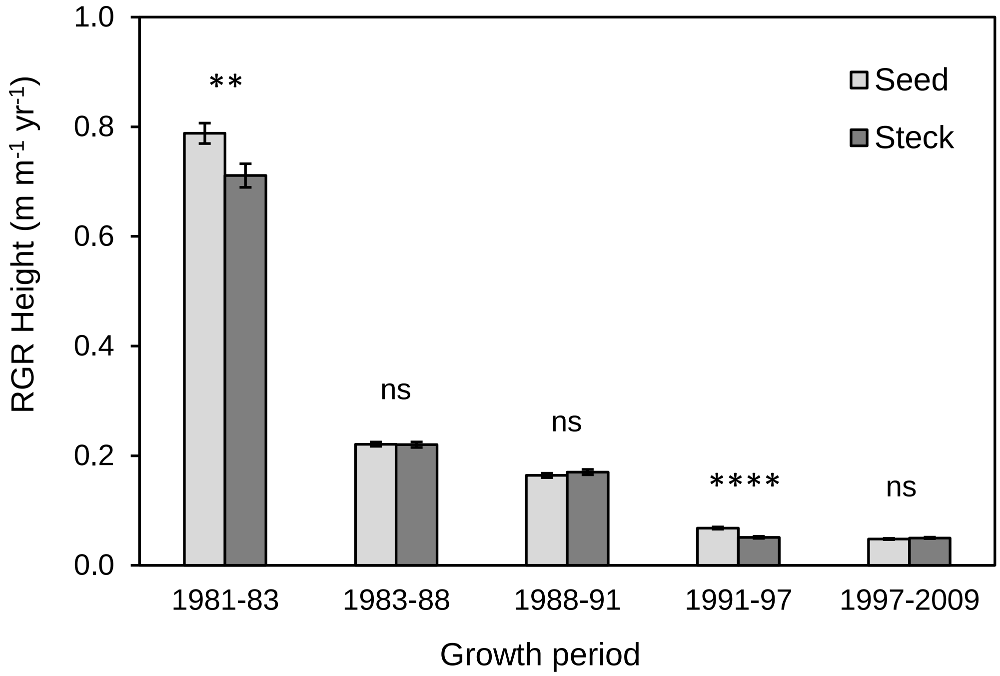


Figure 48. Trial 1 seedling (Seed; n = 68) and steckling (Steck; n = 63) mean relative growth rate (RGR) for five growth periods over 29 growing seasons at Foresthill Seed Orchard. Only grove samples with both seedlings and stecklings were included in this analysis. Tests of significance were conducted using the non-parametric Kruskal-Wallis test. Levels of significance for each growth period indicated by asterisks (ns = no significance; * $p < 0.05$; ** $p < 0.01$; *** $p < 0.001$; **** $p < 0.0001$).

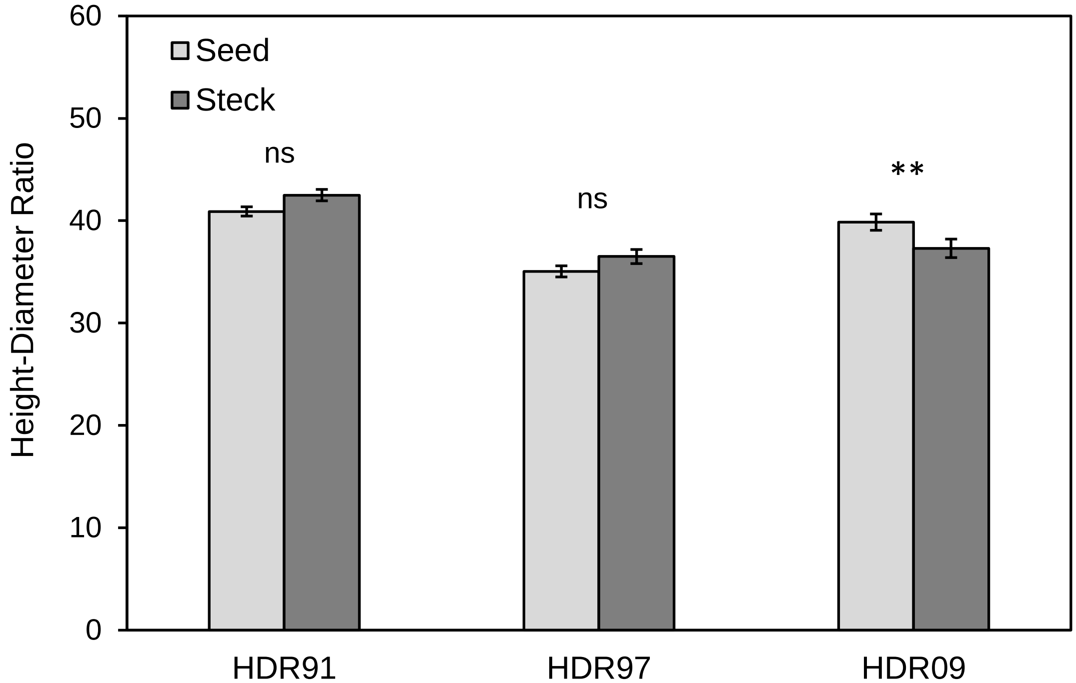


Figure 49. Trial 1 seedling (Seed; n = 68) and steckling (Steck; n = 63) height-diameter ratio for three measurement years over from 1991 to 2009 at Foresthill Seed Orchard. Only grove samples with both seedlings and stecklings were included in this analysis. Tests of significance were conducted using the non-parametric Kruskal-Wallis test. Levels of significance for each growth period indicated by asterisks (ns = no significance; * $p < 0.05$; ** $p < 0.01$; *** $p < 0.001$; **** $p < 0.0001$).

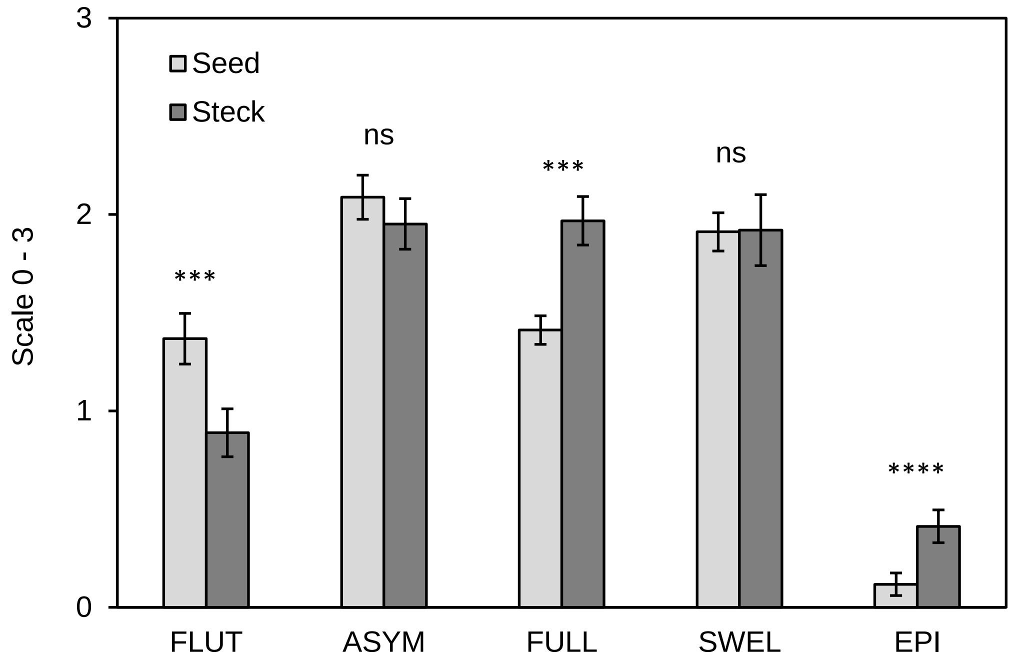


Figure 50. Trial 1 seedling (Seed; n = 68) and steckling (Steck; n = 63) form traits assessed in 2009 after 29 growing seasons at Foresthill Seed Orchard. Form traits assessed on a four point scale (0 = weaker; 3 = stronger). Only grove samples with both seedlings and stecklings were included in this analysis. Tests of significance were conducted using the non-parametric Kruskal-Wallis test. Levels of significance for each trait indicated by asterisks (ns = no significance; * $p < 0.05$; ** $p < 0.01$; *** $p < 0.001$; **** $p < 0.0001$).

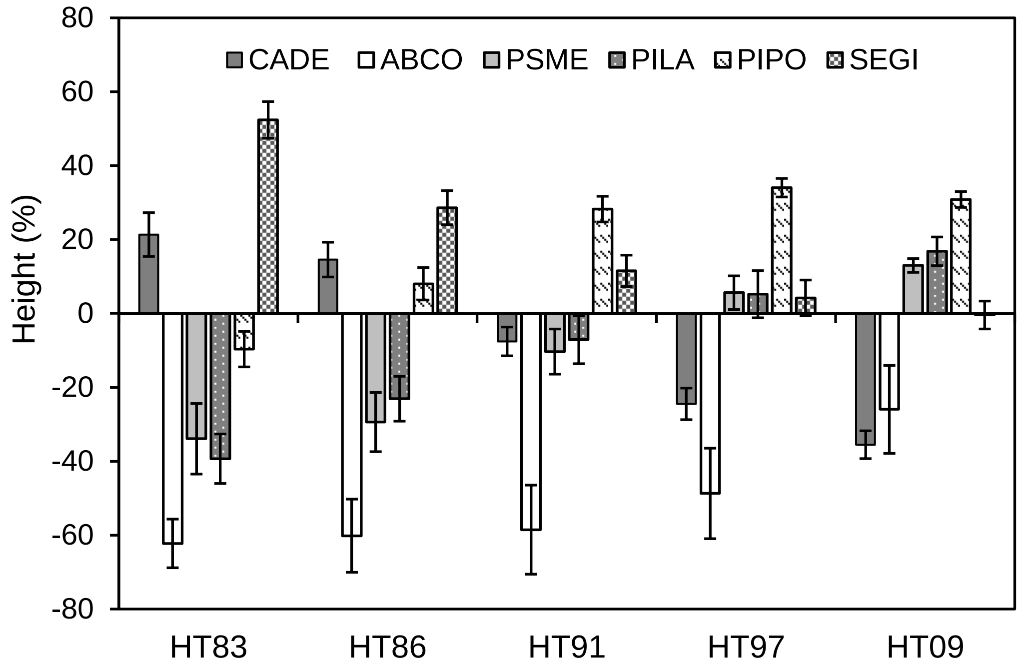


Figure 51. Trial 2 SEGI and mixed conifer seedling height (HT) in percent above or below mean by species in five measurement years from 1983 to 2009 at Foresthill Seed Orchard. Species were incense-cedar (CADE), white fir (ABCO), Douglas-fir (PSME), sugar pine (PILA), ponderosa pine (PIPO), and giant sequoia (SEGI). Error bars are relative standard errors of the species mean, where the standard error is divided by the mean and expressed as a percent (%).

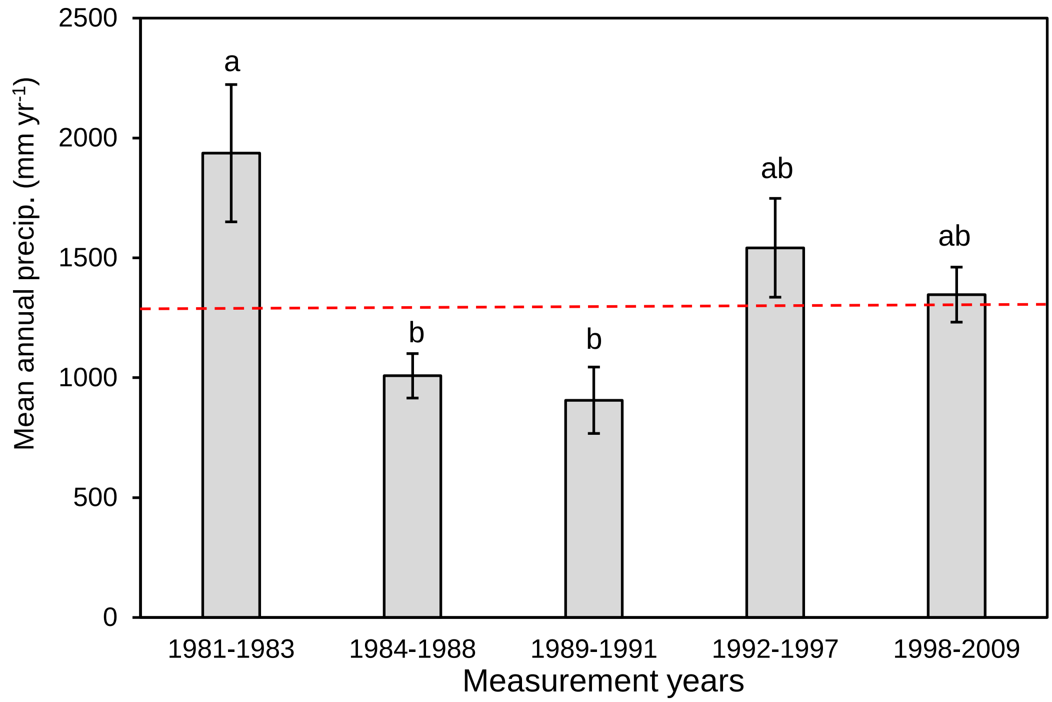


Figure 52. Mean annual periodic precipitation at Foresthill, CA approximately eight km west of FSO study site for periods corresponding to five measurement periods at FSO. Letters indicate significant differences among measurement years at $\alpha < 0.05$. Horizontal line across figure indicates 30-year mean precipitation at Foresthill (1300 mm).

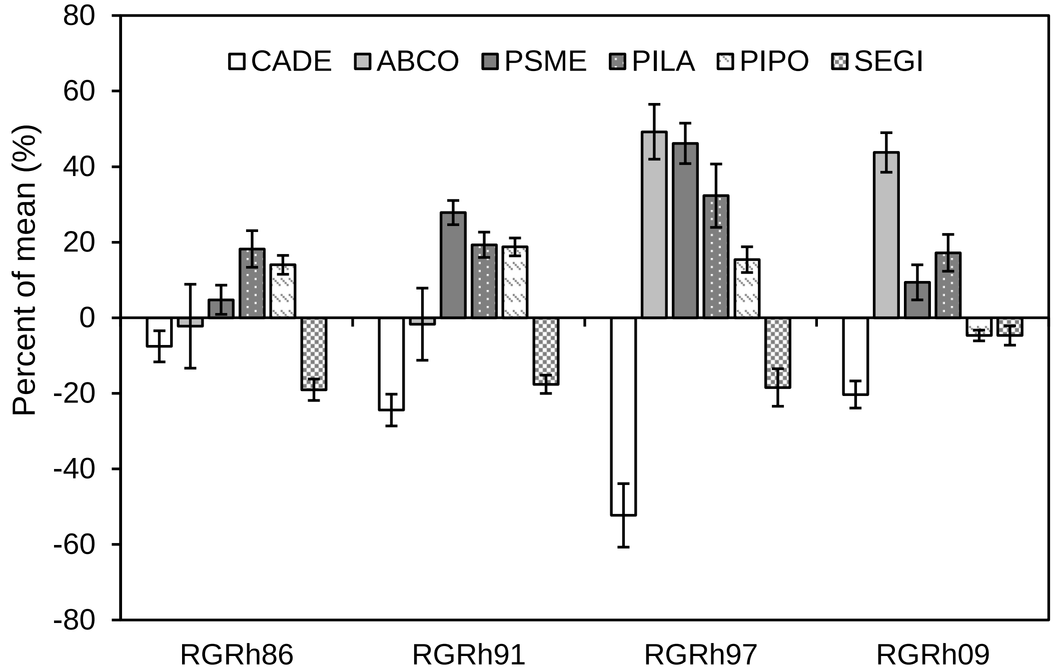


Figure 53. Trial 2 SEGI and mixed conifer seedling mean periodic relative height growth rate (RGRh) in percent above or below mean by species for four measurement periods from 1983 to 2009 at Foresthill Seed Orchard. Relative growth rates were calculated between consecutive measurements in 1983-86, 1986-1991, 1991-97, and 1997-09. Species were incense-cedar (CADE), white fir (ABCO), Douglas-fir (PSME), sugar pine (PILA), ponderosa pine (PIPO), and giant sequoia (SEGI). Error bars are relative standard errors of the species mean, where the species standard error is divided by the mean and expressed as a percent (%).

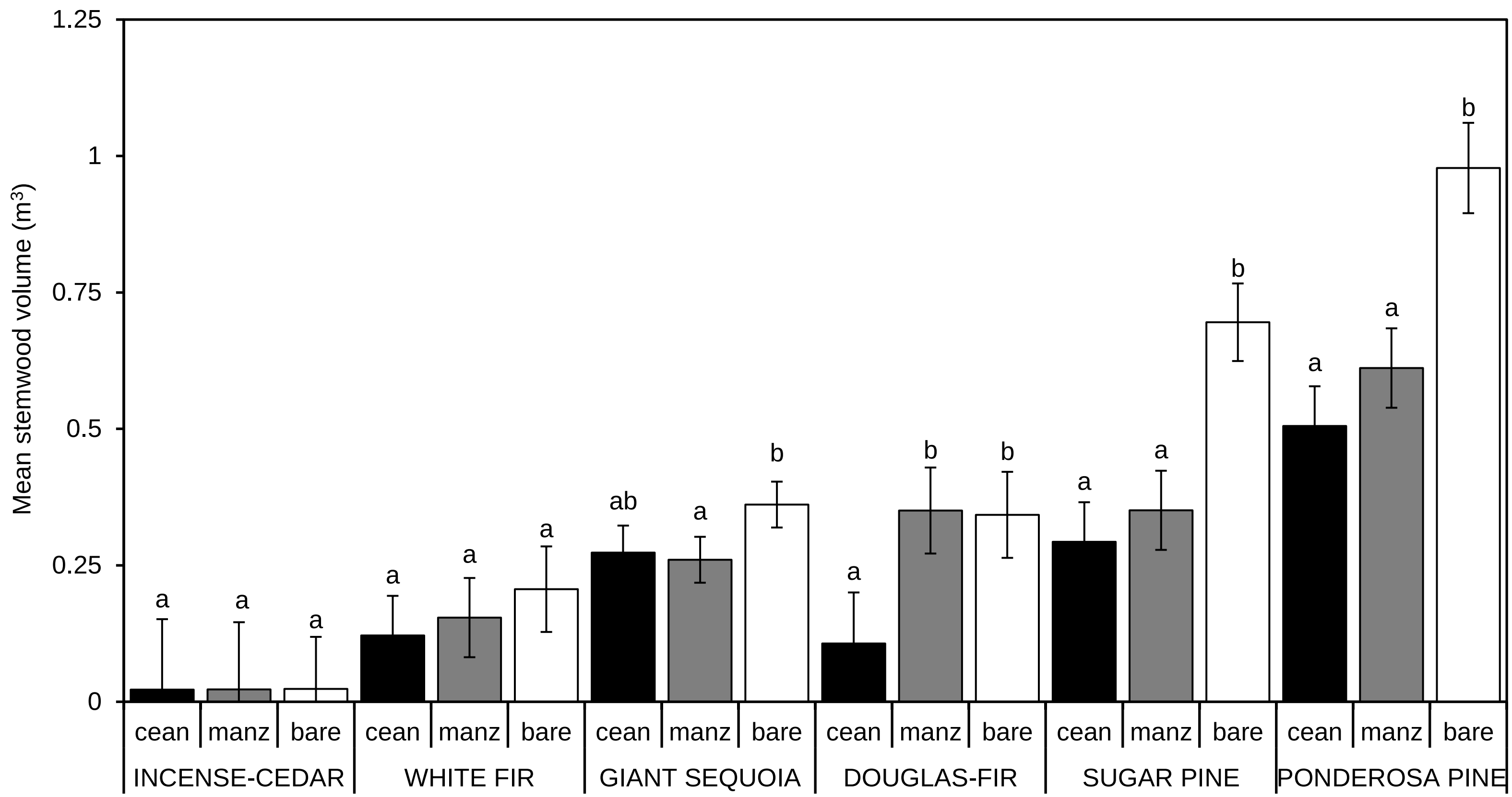


Figure 54. Trial 3 SEGI and mixed conifer mean stemwood volume (m^3) of six conifer species growing with either *Ceanothus* (cean), *Arctostsphylos* (manz), or bare ground without shrubs (bare). Volume assumes conic stem form. Significant differences at $\alpha = 0.05$ in mean estimates of volume for species by treatment are indicated by letter groups. Within conifer species differences indicated only.

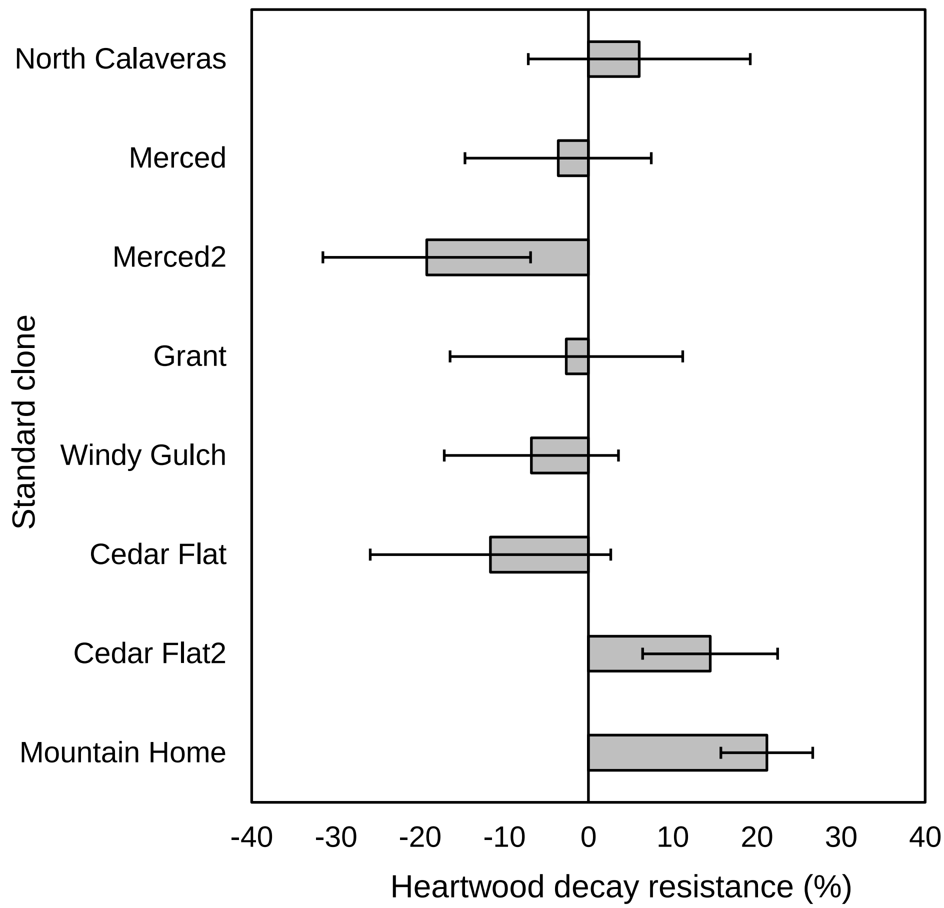


Figure 55. Trial 1 heartwood decay resistance of SEGI standard clone stumps thinned in 1999 in percent above or below the mean heartwood decay resistance score assigned in 2010, 11 years after thinning at Foresthill Seed Orchard.

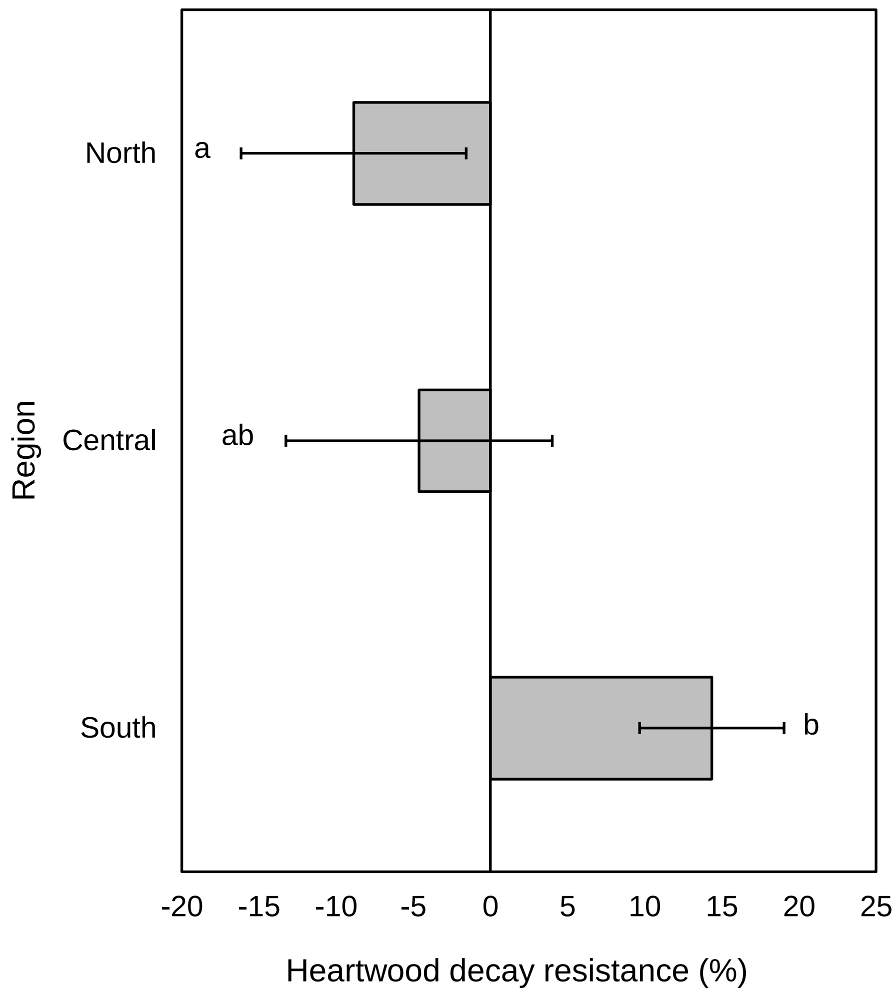


Figure 56. Heartwood decay of standard clones by region – trial 1 heartwood decay resistance of SEGI standard clone stumps thinned in 1999 by region of clone origin in the native range in percent above or below mean at Foresthill Seed Orchard. Differences among-regions were significant ($p \leq 0.05$). Letters indicate significant differences among-regions in multiple comparison test. Number of stumps assessed were: north = 41, central = 27, south = 34 stumps.

LITERATURE CITED

Ahuja, M.R. 2008. Genetic constitution and diversity in four narrow endemic redwoods from the family Cupressaceae. Euphytica 165:5-19.

Aitken, S.N., S. Yeaman, J.A. Holliday, T. Wang, and S. Curtis-McLane. 2008. Adaptation, migration or extirpation: climate change outcomes for tree populations. Evolutionary Applications 1(1): 95-111.

Anderson, R.S. 1994. Paleohistory of a giant sequoia grove: the record from Log Meadow, Sequoia National Park. USDA Forest Service General Technical Report PSW-151. 7 p.

Anderson, R.S. and S.J. Smith. 1994. Paleoclimatic interpretations of meadow sediment and pollen stratigraphies from California. Geology 22:723-726.

Atwater, B.F., D.P. Adam, J.P. Bradbury, R.M. Forester, R.M. Mark, W.R. Lettis, G.R. Fisher, K.W. Gobalet, and S.W. Robinson. 1986. A fan dam for Tulare Lake, California, and implications for the Wisconsin glacial history of the Sierra Nevada. Geological Society of America Bulletin 97:97-109.

Axelrod, D.I. 1959. Late cenozoic evolution of the Sierran Big Tree forest. Evolution. 13(1): 9-23.

Bergin, D.O., M.O. Kimberley, C.B. Low. 2008. Provenance variation in Podocarpus totara (D. Don): Growth, tree form and wood density on a coastal site in the north of the natural range, New Zealand. Forest Ecology and Management 255(5): 1367-1378.

Bergmann, F. 1978. The allelic distribution at an acid phosphatase locus in Norway spruce (Picea abies) along similar climatic gradients. Theoretical and Applied Genetics 52(2): 57-64.

Blackman, V.H. 1919. The compound interest law and plant growth. Annals of Botany. 33:353-360.

Bonnicksen, T.M., and E.C. Stone. 1982. Reconstruction of a pre-settlement giant sequoia-mixed conifer forest community using the aggregation approach. Ecology 1134-1148.

Bouvet, J.M., P.H. Vigneron, R. Gouma, and A. Saya. 2003. Trends in variances and heritabilities with age for growth traits in *Eucalyptus* spacing experiments. Silvae Genetica 52(3-4): 121-132.

Brand, D.G. 1991. The establishment of boreal and sub-boreal conifer plantations: an integrated analysis of environmental conditions and seedling growth. Forest Science 37:68-100.

Burdon, R.D., and G.B. Sweet. 1976. The problem of interpreting inherent differences in tree growth shortly after planting. P. 483-502 in Cannell, M.G.R. (Ed.) Tree physiology and yield improvement. Academic Press, London.

Burdon, R.D., and C.B. Low. 1992. Genetic survey of Pinus radiata. 6. Wood Properties: variation, heritabilities, and interrelationships with other traits. New Zealand Journal of Forest Science 22: 228-245.

Burnham, K. P., and Anderson, D. R. 2002. Model selection and multi-model inference: a practical information-theoretic approach. Springer-Verlag. New York. 488 p.

Cole, K. 1983. Late Pleistocene vegetation of Kings Canyon, Sierra Nevada, California. Quaternary Research 19: 117-129.

Conkle, M.T. 1973. Growth data for 29 years from the California elevational transect study of ponderosa pine. Forest Science 19(1): 31-39.

Conover, W.J., M.E. Johnson, and M.M. Johnson. 1981. A comparative study of homogeneity of variances, with application to the outer continental shelf bidding data. Technometrics 23: 351-361.

Cornelius, J. 1994. Heritabilities and additive genetic coefficients of variation in forest trees. Canadian Journal of Forest Research 24: 372-379.

Davis, O.K. 1999. Pollen analysis of Tulare Lake, California: Great Basin-like vegetation in Central California during the full glacial and early Holocene. Review of Paleobotany and Palynology 107: 249-257.

Davis, O.K. and M.J. Moratto. 1988. Evidence of a warm dry early Holocene in the western Sierra Nevada of California: Pollen and plant macrofossil analysis of Dinkey and Exchequer Meadows. Madrono 35:132-149.

De La Mare, P. 2004. *Sequoiadendron* P. 11-14 in The proceedings of a farm forestry seminar on special purpose tree plantings. New Zealand Farm Forestry Association. Telford Polytechnic, New Zealand.

Deal, R.L., R.J. Barbour, M.H. McClellan, and D.L. Parry. 2003. Development of epicormic sprouts in Sitka spruce following thinning and pruning in south-east Alaska. Western Journal of Applied Forestry 76(4): 401-412.

DeBell, J.D. and B.L. Gartner. 1997. Stem characteristics on the lower log of 35-year-old western redcedar grown at several spacings. Western Journal of Applied Forestry 12(1): 9-15.

Dekker-Robertson, D.L. and J. Svolba. 1991. Results of a *Sequoiadendron giganteum* [(Lindl.) Buch.] provenance experiment in Germany. Silvae Genetica 42(4-5): 199-206.

Dodd, R.S. and R. DeSilva. 2016. Long-term demographic decline and late glacial divergence in a Californian paleoendemic: *Sequoiadendron giganteum* (giant sequoia). Ecology and Evolution 6(10): 3342-3355.

Dolanc C.R., R.D. Westfall, H.D. Safford, J.H. Thorne, and M.W. Schwartz. 2013. Growth-climate relationship for six subalpine tree species in a Mediterranean climate. Canadian Journal of Forest Research 43: 1114-1126.

Du, W., and L. Fins. 1989. Genetic variation among five giant sequoia populations. Silvae Genetica 38(2): 70-76.

Dunne, J.A. and V.T. Parker. 1999. Species-mediated soil moisture availability and patchy establishment of *Pseudotsuga menziesii* in chaparral. Oecologia 119: 36-45

Falconer, D.S. and T.F.C. Mackay. 1996. Introduction to quantitative genetics. Longman, Essex, England. 480 p.

Fins, L. 1979. Genetic architecture of giant sequoia. PhD Dissertation. University of California, Berkeley 237 p.

Fins, L., and W.J. Libby. 1982. Population variation in *Sequoiadendron*: Seed and seedling studies, vegetative propagation, and isozyme variation. Silvae Genetica 31(4): 102-110.

Fins, L., and W.J. Libby. 1994. Genetics of giant sequoia. USDA Forest Service General Technical Report PSW-151. 4 p.

Fisher, R.A. 1930. The genetical theory of natural selection. Clarendon Press, Oxford, U.K. 318 p.

Foster, G.S., R.K. Campbell, W.T. Adams. 1984. Heritability, gain, and C effects in rooting of western hemlock cuttings. Canadian Journal of Forest Research 14(5): 628-638.

Fowells, H.A. 1941. The period of seasonal growth of ponderosa pine and associated species. Journal of Forestry 39(7): 601-608.

Franklin, E.C. Model relating levels of genetic variance to stand development of four North American conifers. Silvae Genetica 28(5-6): 207-212.

Guinon, M., J.B. Larson and W. Spethmann. 1982. Frost resistance and early growth of *Sequoiadendron giganteum* seedlings of different origins. Silvae Genetica 31: 173-178.

Hagerman, S.M. and D.M. Durall. 2003. Ectomycorrhizal colonization of greenhouse-grown Douglas-fir (*Pseudotsuga menziesii*) seedlings by inoculum associated with roots of refuge plants sampled from a Douglas-fir forest in the southern interior of British Columbia. Canadian Journal of Botany 82: 742-751.

Hamrick, J.L. 1976. Variation and selection in western montane species II. Variation within and between populations of white fir on an elevational transect. Theoretical and Applied Genetics 47(1): 27-34.

Hamrick, J.L., and W.J. Libby. 1972. Variation and selection in western U.S. montane species. Silvae Genetica 21:29-35.

Hamrick, J.L., J.B. Mitton, and Y.B. Linhart. 1981. Levels of genetic variation in trees: influence of life history characteristics P. 35-41 in Isozymes of North American forest trees and forest insects. M.T. Conkle (ed.). U.S. Forest Service Berkeley, California.

Hamrick, J.L., M.J.W. Godt, and S.L. Sherman-Broyles. 1992. Factors influencing levels of genetic diversity in woody plant species. New Forests 6: 95-124.

Hannrup, B., C. Cahalan, G. Chantre, M. Grabner, B. Karlsson, I. Le Bayon, G. Llyod Jones, U. Mueller, H. Pereira, J. Rodrigues, S. Rosner, P. Rozenberg, L. Wilhelmsson, R. Wimmer. 2004. Genetic parameters of growth and wood quality traits in *Picea abies*. Scandinavian Journal of Forest Research 19(1):14-29.

Harry, D.E. 1987. Shoot elongation and growth plasticity in incense-cedar. Canadian Journal of Forest Research 17(6): 484-489.

Hartesveldt, R.J., H.T.Harvey, H.S. Shellhammer, and R.E. Stecker. 1975. The giant sequoia of the Sierra Nevada. Washington, DC: U.S. Department of Interior. 180 p.

Harvey, H.T., 1985. Evolution and history of giant sequoia. P. 1-3 in Proceedings of the Workshop on Management of Giant Sequoia, Weatherspoon, C.P., Iwamoto, Y.R., Piirto, D.D. (eds.). PSW GTR-95, USDA For. Serv.

Harvey, H.T. 1986. Evolution and history of giant sequoia. General Technical Report PSW-95. Berkeley, CA. Pacific Southwest Forest and Range Experiment Station, Forest Service, U.S. Department of Agriculture.

Harvey, H.T. H.S. Shellhammer, and R.E. Stecker. 1980. Giant sequoia ecology. U.S. Department of Interior, National Park Service. Scientific Monograph Series. 12, Washington DC, 182 p. Accessed online: http://www.nps.gov/history/history/online_books/science/12/index.htm; last accessed: April 17, 2016.

Hayhoe, K., D. Cayan, C.B. Field, P.C. Frumhoff, E.P. Maurer, N.L. Miller, S.C. Moser, S.H. Schneider, K.N. Cahill, E.E. Cleland, L. Dale, R. Drapek, R.M. Hanemann, L.S. Kalkstein, J. Lenihan, C.K. Lunch, R.P. Neilson, S.C. Sheridan, and J.H. Verville. 2004. Emissions pathways, climate change, and impacts on California. P.N.A.S. 101(34): 12422–12427.

Heald, R.C. and T.M. Barrett. 1999. Effects of planting density on early growth of giant sequoia (*Sequoiadendron giganteum*). Western Journal of Applied Forestry 14(2): 65-72.

Henderson, L.T., T.F. Koppe, and R.E. Schoenike. 1979. Ten-year evaluation of a seed source study of eastern redcedar in South Carolina. Tree Planters' Notes 30(3): 3-6.

Horton, T.R., Bruns, T.D. and Parker, V.T. 1999. Ectomycorrhizal fungi associated with *Arctostaphylos* contribute to *Pseudotsuga menziesii* establishment. Canadian Journal of Botany 77: 93-102.

Howard, J.L. 1992. *Arctostaphylos viscida*. In: Fire Effects Information System, [Online]. U.S. Department of Agriculture, Forest Service, Rocky Mountain Research Station, Fire Sciences Laboratory (Producer). Available online: http://www.fs.fed.us/database/feis/; last accessed: May 10, 2016.

IPCC. 2007: Climate Change 2007: Synthesis Report. Contribution of Working Groups I, II and III to the Fourth Assessment Report of the Intergovernmental Panel on Climate Change [Core Writing Team, Pachauri, R.K and Reisinger, A. (eds.)]. IPCC, Geneva, Switzerland, 104 p. Available online: http://www.ipcc.ch/ipccreports/ar4-syr.htm; last accessed: October 29, 2015.

Jansson, G., L. Bailan, and B. Hannrup. 2003. Time trends in genetic parameters for height and optimal age for parental selection in Scots pine. Forest Science. 49(5): 696-705.

Johnson, G.R., R.A. Sniezko, and N.L. Mandel. 1997. Age trends in Douglas-fir genetic parameters and implications for optimum selection age. Silvae Genetica 46(6): 349-358.

Julin, K.R., C.G. Shaw III, W.A. Farr, and T.M. Hinckley. 1993a. The fluted western hemlock of Alaska. I. Morphological studies and experiments. Forest Ecology and Management 60(1): 119-132.

Julin, K.R., C.G. Shaw III, W.A. Farr, and T.M. Hinckley. 1993b. The fluted western hemlock of Alaska. II. Stand observations and synthesis. Forest Ecology and Management 60(1): 133-141.

Kellogg, R.M., and F.J. Barber. 1981. Stem eccentricity in coastal western hemlock. Canadian Journal of Forest Research 11(3): 715-718.

Kijidani, Y., T. Hamazuna, S. Ito, R. Kitahara, S. Fukuchi, N. Mizoue, and S. Yoshida. 2010. Effect of height-diameter ratio on stem stiffness of sugi (*Cryptomeria japonica*) cultivars. Journal of Wood Science 56(1): 1-6.

Kitzmiller, J.H. 2004. Adaptive genetic variation in sugar pine. P. 23-27 in Breeding and Genetic Resources of Five-Needled Pines: Growth,

adaptability, and pest resistance. Sniezko, R.A., S. Samman, S.E. Schlarbaum, and H.B. Kriebel (eds.), IUFRO Working Party 2(15).

Kitzmiller, J.H. 2005. Provenance trials of ponderosa pine in Northern California. Forest Science 51(6): 595-607.

Kitzmiller, J.H., and G. Lunak. 2012. Growth of Giant Sequoia Compared to Ponderosa Pine and Other Mixed-Conifers in California Plantations. Western Journal of Applied Forestry 27(4): 196-204.

Knigge, W. 1993. Giant sequoia (*Sequoiadendron giganteum* (Lindl.) Buchholz) in Europe. Holz als Roh- und Werkstoff 51: 145-155.

Kough, J.L., R. Molina, and R.G. Linderman. 1985. Mycorrhizal responsiveness of *Thuja*, *Calocedrus*, *Sequoia*, and *Sequoiadendron* species of western North America. Canadian Journal of Forest Research 15: 1049-1054.

Kovacic, D.A., T.V. St. John, and M.I. Dyer. 1984. Lack of vesicular-arbuscular mycorrhizal inoculums in a ponderosa pine forest. Ecology 65(6):1755-1759.

Kozlowski, T.T., and S.G. Pallardy. 1997. Physiology of woody plants. 2nd edition. Academic Press, Inc. San Diego, CA. 411 p.

Krakowski, J., and M.U. Stoehr. 2009. Coastal Douglas-fir provenance variation: patterns and predictions for British Columbia seed transfer. Annals of Forest Science 66: 811.

Ledig, F.T., and M.T. Conkle. 1983. Gene diversity and genetic structure in a narrow endemic, Torrey pine (*Pinus torreyana* Parry ex Carr.). Evolution 37(1): 79-85.

Leimu, R., P. Mutikainen, and J. Koricheva, M. Fischer. 2006. How general are positive relationships between plant population size, fitness, and genetic variation? Journal of Ecology 94(5): 942-952.

Levine, C.R., F. Krivak-Tetley, N.S. van Doorn, J.S. Ansley, and J.J. Battles. 2016. Long term demographic trends in a fire suppressed mixed conifer forest. Canadian Journal of Forest Research 46: 745-752.

Li, P, J. Beaulieu, A. Corriveau, and J. Bousquet. 1993. Genetic variation in juvenile growth and phenology in a white spruce provenance-progeny test. Silvae Genetica 42(1): 52-60.

Libby, W.J. 1986. Genetic variation and early performance of giant sequoia in plantation. Gen. Tech. Rep. PSW-95. Berkeley, CA. Pacific Southwest Forest and Range Experiment Station, Forest Service, U.S. Department of Agriculture.

Libby, W.J., and C.C. Cockerham. 1980. Random non-contiguous plots in interlocking field layouts. Silvae Genetica 29(5-6): 183-190.

Littell, R.C., G.A. Milliken, W.W. Stroup, R.D. Wolfinger, and O. Schabenberger. 2006 SAS for mixed models. SAS Institute Inc., Cary, NC, USA.

Mahalovich, M.F. 1985. A genetic architecture study of giant sequoia: early growth characteristics. MS Thesis. Wildland Resource Science, University of California, Berkeley, California 98 p.

Melchior, G.H. and S. Herrmann. 1987. Differences in growth performance of four provenances of Giant Sequoia (*Sequoiadendron giganteum* (Lindl.)Buchh.). Silvae Genetica 36(2): 65-68.

Millar C.I., and W.J. Libby. 1989. Disneyland or native ecosystem: genetics and the restorationist. Ecological Restoration. 7(1): 18-24.

Millar C.I., and W.J. Libby. 1991. Strategies for conserving clinal, ecotypic, and disjunct population diversity in widespread species. P. 149-170 in: Genetics and Conservation of Rare Plants Falk DA, K.E. Holsinger (eds.). Oxford University Press, UK. Accessed online: http://www.fs.fed.us/psw/publications/millar/psw_1991_millar001.pdf; last accessed: April, 17, 2016.

Millar, C.I., and W.B. Woolfenden. 1999. Sierra Nevada Forests: Where did they come from? Where are they going? What does it mean? P. 206-236 in Transcripts of 64th North American Wildlands and Natural Resources Conference.

Molina, R. 1994. The role of mycorrhizal symbioses in the health of giant redwoods and other forest ecosystems. USDA Forest Service General Technical Report PSW-151: 78-81.

Mote, P.W. 2006. Climate-driven variability and trends in mountain snowpack in western North America. Journal of Climate 19: 6209-6220.

Mueller-Starck, G., P. Baradat, and F. Bergmann. 1992. Genetic variation within European tree species. New Forests 6(1-4): 23-47.

Namkoong, G., R.A. Usanis, and R.R. Silen. 1972. Age-related variation in genetic control of height growth in Douglas-fir. Theoretical and Applied Genetics 42(4): 151-159.

Namkoong, G., and M.T. Conkle. 1976. Time trends in genetic control of height growth in ponderosa pine. Forest Science 22: 2-12.

O'Hara, K.L., and J-P. Berrill. 2009. Epicormic sprout development in pruned coast redwood: pruning severity, genotype, and sprouting characteristics. Annals of Forest Science 66(4): 409-409.

O'Hara, K.L., R.A. York, and R.C. Heald. 2008. Effect of pruning severity and timing of treatment on epicormic sprout development in giant sequoia. Western Journal of Applied Forestry 81(1):103-110.

Paques, L.E. 2001. Genetic control of heartwood content in larch. Silvae Genetica 50: 2 69-75.

Paul, S., F.N. Wachira, W. Powell, and R. Waugh. 1997. Diversity and genetic differentiation among populations of In

Peracca, G., and K.L. O'Hara. 2008. Effects of growing space on growth for 20-year-old giant sequoia, ponderosa pine and Douglas-fir in the Sierra Nevada. Western Journal of Applied Forestry 23(3): 156-165.

Piirto, D.D. 1986. Wood of giant sequoia: properties and unique characteristics. Gen. Tech. Rep. PSW-95. Berkeley, CA. Pacific Southwest Forest and Range Experiment Station, Forest Service, U.S. Department of Agriculture.

Piirto, D.D., and R.R. Rogers. 2002. An ecological basis for managing giant sequoia ecosystems. Environmental Management 30(1): 110-128.

Power, M.J. 1998. Paleoclimatic interpretations of an alpine lake in southcentral Sierra Nevada. M.S. Thesis, Northern Arizona University. Flagstaff. 93 p. [in Millar and Woolfenden, 1999]

Raven, P.H., and D.I. Axelrod. 1978. Origin and relationships of the California flora, Volume 72. University of California Press 134 p.

Ray, R.L. 2016. Moisture stress indicators in giant sequoia groves in the Southern Sierra Nevada of California, USA. Vadose Zone Journal 15(10): 1-19.

Raymond, C.A., and M. Henson. 2009. Genetic variation amongst and within the native provenances of *Pinus radiata* D. Don in South-eastern Australia. 1. Growth and form to age 26 years. Silvae Genetica 58(5): 242.

Rose S. L. 1980 Mycorrhizal associations of some actinomycete nodulated nitrogen-fixing plants. Canadian Journal of Botany 58 (13): 1449-1454.

Rundel, P.W. 1969. An annotated list of the groves of *Sequoiadendron giganteum* in the Sierra Nevada, California. Research Report. Sequoia and Kings Canyon National Park files. 15 p.

Rundel, P.W. 1971. Community structure and stability in the giant sequoia groves of the Sierra Nevada, California. American Midland Naturalist 85(2):478-492.

Rundel, P.W. 1972. Habitat restriction in giant sequoia: the environmental control of grove boundaries. American Midland Naturalist 87(l): 81-99.

Rydelius, J.A., and W.J. Libby. 1993. Arguments for clonal redwood forestry. P. 158-168 in Clonal Forestry II. Ahuja, M.A., and W.J. Libby (eds.) Springer Berlin Heidelberg.

SAS Institute Inc. 2008. SAS® Version 9.2. SAS Institute Inc. Cary, NC, USA.

Sorensen, F.C., and T.L. White. 1988. Effect of inbreeding on variance structure in tests of wind-pollination Douglas-fir progenies. Forest Science 34(1): 102-118.

South, D.B., J.G. Mexal, and J.P. van Buijtenen. 1988. The relationship between seedling diameter at planting and long term volume growth of loblolly pine seedlings in east Texas P. 1-11 in Proceedings of the Tenth North

American Forest Biology Workshop, Worral, J., J. Loo-Dinkinns, and D.T. Lester (eds.). Vancouver, B.C. 255 p.

Stephenson, N.L. 1994. Long-term dynamics of giant sequoia populations: Implications for managing a pioneer species. P. 56-63 in Proceedings of the Symposium on Giant Sequoias: Their Place in the Ecosystem and Society, Aune, P. (ed.) General Technical Report PSW-151. Albany, California. 170 p.

Stohlgren, T.J. 1993. Spatial patterns of giant sequoia (*Sequoiadendron giganteum*) in two sequoia groves in Sequoia National Park, California. Canadian Journal of Forest Research 23(2):120-132.

Sugiura, N. 1978. Further analysis of the data by Akaike's information criterion and the finite corrections. Communications in Statistics, Theory and Methods A7:13-26.

Sweet, G.B., and L.G. Wells. 1974. Comparison of the growth of vegetative propagules and seedlings of *Pinus radiata*. New Zealand Journal of Forest Science. 4: 399-409.

Tappeiner, J.C., II. 1980. Sierra Nevada Mixed Conifer 243. P. 118-119 in Forest cover types of the United States and Canada. Eyre, F.H. ed. Soc. Amer. Foresters, Washington D.C.

Thornton, P.E., M.M. Thornton, B.W. Mayer, N. Wilhelmi, Y. Wei, and R.B. Cooke. 2013. Daymet: Daily surface weather on a 1 km grid for North America 1980 -2011. Accessed online: http://daymet.ornl.gov/ on 03/20/2013 from Oak Ridge National Laboratory Distributed Active Archive Center, Oak Ridge, Tennessee, U.S.A. doi:10.3334/ORNLDAAC/Daymet_V2; last accessed: February 24, 2016.

van Mantgem, P.J., N.L. Stephenson, J.C. Byrne, L.D. Daniels, J.F. Franklin, P.Z. Fule, M.E. Harmon, A.J. Larson, J.M. Smith, A.H. Taylor, and T.T. Veblen. 2009. Widespread increase of tree mortality rates in the western United States. Science 323: 521–524.

Waghorn, M.J., M.S. Watt, E.G. Mason. 2007. Influence of tree morphology, genetics, and initial stand density on outerwood modulus of elasticity of 17-year old *Pinus radiata*. Forest Ecology and Management 244(1): 86-92.

Wareing, P.F. 1966. The physiologist's approach to tree growth. Forestry Supplement 7-18.

Waring, K.M., and K.L. O'Hara. 2005. Ten-year growth and epicormic sprouting response of western larch to pruning in western Montana. Western Journal of Applied Forestry 20(4): 228-232.

Weatherspoon, C. 1990. *Sequoiadendron giganteum* (Lindl.) Buchholz. P. 552-562 in Silvics of North America. Vol. 1. Conifers. Eds. R.M. Burns and B.H. Honkala. Agric. Handbk. 654, USDA Forest Service, Washington, DC. Available online: http://www.na.fs.fed.us/spfo/pubs/silvics_manual/table_of_contents.htm; last accessed: May 9, 2016.

Western Regional Climate Center. 2014. Cooperative Climatological Data Summaries. Available online: http://www.wrcc.dri.edu/climatedata/climsum/; last accessed: Feb. 23, 2014.

Wheeler, N.C., and R.P. Guries. 1982. Population structure, genic diversity, and morphological variation in *Pinus contorta* Dougl. Canadian Journal of Forest Research 12(3): 595-606.

White, T.L., W.T. Adams. D.B. Neale. 2007. Forest Genetics. CABI. 704 p.

Willard, D. 2000. A guide to the sequoia groves of California. Yosemite Association. El Portal, California. 124p.

Williamson, R.L. 1975. Out-of-roundness in Douglas-fir stems. Forest Science. 21(4): 365-370.

Wright, J.W. 1970. Genetics of eastern white pine. Research Papers. United States Forest Service WO-9.

Yeh, F.C., W.M. Cheliak, B.P. Dancik, K. Illingworth, D.C. Trust, and B.A. Pryhitka. 1985. Population differentiation in lodgepole pine, Pinus contorta spp. Latifolia: a discriminant analysis of allozyme variation. Canadian Journal of Genetics and Cytology 27(2): 210-218.

York, R.A., J.J. Battles, A.K. Eschtruth, F.G. Schurr. 2009. Giant sequoia (*Sequoiadendron giganteum*) regeneration in experimental canopy gaps. Restoration Ecology. 19(1): 14-23.

York, R.A., D. Fuchs, J.J. Battles, and S.L. Stephens. 2010. Radial growth responses to gap creation in large, old *Sequoiadendron giganteum*. Applied Vegetation Science 13(4): 498-509.

York, R.A., N.L. Stephenson, M. Meyer, S. Hanna, T. Moody, T. Carrio, and J.J. Battles. 2013a. Giant Sequoia in C.A. Sydoriak et al. (eds.), A natural resource condition assessment for Sequoia and Kings Canyon National Parks. Nat. Resor. Rep. NPS/SEKI/NRR-2013/665.11a. National Park Service, Fort Collins, CO. 81 p.

York, R.A., K.L. O'Hara, and J.J. Battles. 2013b. Density effects on giant sequoia (*Sequoiadendron giganteum*) growth through 22 years: Implications for restoration and plantation management. Western Journal of Applied Forestry 28(1): 30-36

Zuur, A.F., E.N. Ieno, and C.S. Elphick. 2010. A protocol for data exploration to avoid common statistical problems. Methods in Ecology and Evolution 1(1): 3-14.

APPENDIX

Table 31. Coefficients and fit statistics for linear mixed effects regression of SEGI steckling height (HT09) as a function of SEGI native grove geographic characteristics for native grove area (Area = “GA” in text) and mean distance in latitude degrees from native grove to two nearest sampled native groves (dAvGrv1 = “Dist” in text). Model includes a random effect accounting for pseudo-replication of data within grove samples (Grove). This is the “best model” output depicted in Table 15 and Figure 43 in the text.

```
Linear mixed model fit by maximum likelihood  ['lmerMod']
Formula: HT09 ~ dAvGrv1 + Area + (1 | Grove)

     AIC      BIC   logLik deviance df.resid
   931.6    950.6   -460.8    921.6      329

Scaled residuals:
     Min       1Q   Median       3Q      Max
-2.37054 -0.70711 -0.02486  0.69787  2.68757

Random effects:
 Groups   Name        Variance Std.Dev.
 Grove    (Intercept) 0.0000   0.0000
 Residual             0.9243   0.9614
Number of obs: 334, groups:  Grove, 20

Fixed effects:
              Estimate Std. Error t value
(Intercept)  4.4852409  0.6415743   6.991
dAvGrv1     -0.8840287  0.5271567  -1.677
Area         0.0003533  0.0001052   3.360

Correlation of Fixed Effects:
        (Intr) dAvGr1
dAvGrv1 -0.993
Area    -0.597  0.532
fit warnings:
Some predictor variables are on very different scales: consider
rescaling
```

Table 32. Coefficients and fit statistics for linear mixed effects regression of SEGI steckling height (HT09) as a function of SEGI native grove geographic characteristics for native grove harvest history (HarvY = Harv in text) and latitude-adjusted elevation (AdjEl). Model includes a random effect accounting for pseudo-replication of data within grove samples (Grove). This is the "best model" output depicted in Table 16 and Figure 44 in the text.

```
Linear mixed model fit by maximum likelihood  ['lmerMod']
Formula: HT09 ~ Harv + AdjEl + (1 | Grove)

     AIC      BIC   logLik deviance df.resid
   474.3    489.8   -232.2    464.3      158

Scaled residuals:
     Min       1Q   Median       3Q      Max
-2.30647 -0.70466  0.01125  0.66573  2.32370

Random effects:
 Groups   Name        Variance Std.Dev.
 Grove    (Intercept) 0.000    0.000
 Residual             1.011    1.005
Number of obs: 163, groups:  Grove, 9

Fixed effects:
              Estimate Std. Error t value
(Intercept)  7.3172925  1.3441255   5.444
HarvY        0.2991434  0.1626839   1.839
AdjEl       -0.0022790  0.0008643  -2.637

Correlation of Fixed Effects:
      (Intr) HarvY
HarvY  0.122
AdjEl -0.996 -0.191
```

Table 33. Coefficients and fit statistics of the linear model of SEGI diameter increment (mm) for the period 1997 – 2009 (Dinc MM) as a function of the competition index CIDBH^2 in a 7 m neighborhood circular radius. This is the "best model" output depicted in Table 24 in text.

```
logCIdbh2<-log(CIdbh2_7+1)
> lm.CIdbh2_7<-lm(DincMM~logCIdbh2)
> summary(lm.CIdbh2_7)

Call:
lm(formula = DincMM ~ logCIdbh2)

Residuals:
    Min      1Q  Median      3Q     Max 
-4.8715 -1.3913  0.1155  1.1869  3.4450 

Coefficients:
            Estimate Std. Error t value Pr(>|t|)    
(Intercept)  14.3457     0.6035  23.770  < 2e-16 ***
logCIdbh2    -5.6344     0.6508  -8.658 1.04e-10 ***
---
Signif. codes:  0 '***' 0.001 '**' 0.01 '*' 0.05 '.' 
0.1 ' ' 1 

Residual standard error: 1.817 on 40 degrees of freedom
Multiple R-squared:  0.6521,    Adjusted R-squared: 
0.6434 
F-statistic: 74.96 on 1 and 40 DF,  p-value: 1.037e-10

> AIC(lm.CIdbh2_7)
[1] 173.3265
> AICc(lm.CIdbh2_7)
[1] 173.9581
```

Table 34. Coefficients and fit statistics of the linear model of SEGI diameter increment (mm) for the period 1997 – 2009 (DincMM) as a function of the competition index CIHegyi in a 7 m neighborhood circular radius for 6 mixed conifer species. Species included were giant sequoia (GSHeg7), incense-cedar (ICHeg7), ponderosa pine (PPHeg7), sugar pine (SPHeg7), Douglas-fir (DFHeg7), and white fir (WFHeg7). This output depicts the "full model" of all mixed conifer species in trial 2.

```
lm.spp.Heg7<lm(DincMM~logGSHeg7+logICHeg7+logPPHeg7+logSPHeg7+
logDFHeg7+logWFHeg7)
> summary(lm.spp.Heg7)

Call:
lm(formula = DincMM ~ logGSHeg7 + logICHeg7 + logPPHeg7 +
logSPHeg7 +
    logDFHeg7 + logWFHeg7)

Residuals:
    Min      1Q  Median      3Q     Max
-3.7144 -1.2562  0.2139  1.1330  3.6118

Coefficients:
            Estimate Std. Error t value Pr(>|t|)
(Intercept)  16.2941     0.9064  17.976  < 2e-16 ***
logGSHeg7    -9.0727     1.4351  -6.322 2.91e-07 ***
logICHeg7   -11.2307     4.2816  -2.623 0.012822 *
logPPHeg7   -14.0781     3.3238  -4.236 0.000157 ***
logSPHeg7    -0.7062     2.5123  -0.281 0.780280
logDFHeg7    -4.0408     3.2707  -1.235 0.224882
logWFHeg7   -12.9540     3.4338  -3.773 0.000600 ***
---
Signif. codes:  0 '***' 0.001 '**' 0.01 '*' 0.05 '.' 0.1 ' ' 1

Residual standard error: 1.811 on 35 degrees of freedom
Multiple R-squared:  0.6978,    Adjusted R-squared:  0.6459
F-statistic: 13.47 on 6 and 35 DF,  p-value: 7.416e-08

> vif(lm.spp.Heg7)
logGSHeg7 logICHeg7 logPPHeg7 logSPHeg7 logDFHeg7
 1.236180  1.279952  1.902253  1.674430  1.152697
logWFHeg7
1.094806

> AIC(lm.spp.Heg7)
[1] 177.414
> AICc(lm.spp.Heg7)
[1] 181.7776
```

Table 35. Coefficients and fit statistics of the linear model of SEGI diameter increment (mm) for the period 1997 – 2009 (DincMM) as a function of the individual species competition index CIHegyi in a 7 m neighborhood circular radius for 4 mixed conifer species. Species included were giant sequoia (GSHeg7), incense-cedar (ICHeg7), ponderosa pine (PPHeg7), and white fir (WFHeg7). This is the "best model" output depicted in Table 25 in the text.

```
lm.spp.Heg7<lm(DincMM~logGSHeg7+logICHeg7+logPPHeg7+logWFHeg7)
> summary(lm.spp.Heg7)

Call:
lm(formula = DincMM ~ logGSHeg7 + logICHeg7 + logPPHeg7 +
logWFHeg7)

Residuals:
    Min      1Q  Median      3Q     Max
-3.9199 -1.0252  0.0388  1.2162  3.9416

Coefficients:
            Estimate Std. Error t value Pr(>|t|)
(Intercept)  16.3115     0.9004  18.116  < 2e-16 ***
logGSHeg7    -9.2272     1.4121  -6.535 1.19e-07 ***
logICHeg7   -12.4462     4.1350  -3.010 0.004685 **
logPPHeg7   -15.7013     2.5360  -6.191 3.46e-07 ***
logWFHeg7   -13.0242     3.4005  -3.830 0.000479 ***
---
Signif. codes:  0 '***' 0.001 '**' 0.01 '*' 0.05 '.' 0.1 ' ' 1

Residual standard error: 1.804 on 37 degrees of freedom
Multiple R-squared:  0.683,     Adjusted R-squared:  0.6487
F-statistic: 19.93 on 4 and 37 DF,  p-value: 8.014e-09

> vif(lm.spp.Heg7)
logGSHeg7 logICHeg7 logPPHeg7 logWFHeg7
 1.206464  1.203355  1.116210  1.082290

> AIC(lm.spp.Heg7)
[1] 175.4136
> AICc(lm.spp.Heg7)
[1] 177.8136
```

Table 36. Coefficients and fit statistics for the generalized linear mixed effects model of stemwood volume as a function of conifer tree species (Spp), understory shrub treatment (none, cean, manz), edge or interior planting location (Edge) and their interactions for all edge and interior trees in trial 3. This model output corresponds with Table 27 and Table 28 in text. This model output is depicted in Figure 54 in the text.

Effect	Spp	Treat	Est	s.e.	d.f.	t value	Pr > |t|
Intercept	-	-	0.3607	0.07	1	5.21	0.1207
SPP	ABCO	-	-0.2184	0.11	146	-2.04	0.0434
SPP	CADE	-	-0.3756	0.10	146	-3.7	0.0003
SPP	GS	-	-0.1440	0.08	146	-1.84	0.0680
SPP	PILA	-	0.2578	0.10	146	2.52	0.0129
SPP	PIPO	-	0.5074	0.11	146	4.75	<0.0001
SPP	PSME	-	0.0000	-	-	-	-
TRT	-	cean	-0.1978	0.10	146	-1.95	0.0534
TRT	-	manz	-0.0604	0.11	146	-0.56	0.5737
TRT	-	none	0.0000	-	-	-	-
EDGE	-	1	0.1538	0.04	146	3.94	0.0001
EDGE	-	2	0.0000	-	-	-	-
SPP*TRT	ABCO	cean	0.1218	0.15	146	0.81	0.4178
SPP*TRT	ABCO	manz	0.0171	0.15	146	0.11	0.9113
SPP*TRT	ABCO	none	0.0000	-	-	-	-
SPP*TRT	CADE	cean	0.2160	0.16	146	1.39	0.1665
SPP*TRT	CADE	manz	0.0786	0.15	146	0.51	0.6115
SPP*TRT	CADE	none	0.0000	-	-	-	-
SPP*TRT	GS	cean	0.0708	0.11	146	0.63	0.5324
SPP*TRT	GS	manz	-0.0263	0.12	146	-0.22	0.8242
SPP*TRT	GS	none	0.0000	-	-	-	-
SPP*TRT	PILA	cean	-0.1693	0.15	146	-1.16	0.2487
SPP*TRT	PILA	manz	-0.2488	0.15	146	-1.65	0.1011
SPP*TRT	PILA	none	0.0000	-	-	-	-
SPP*TRT	PIPO	cean	-0.2604	0.15	146	-1.73	0.0853
SPP*TRT	PIPO	manz	-0.2546	0.15	146	-1.66	0.0999
SPP*TRT	PIPO	none	0.0000	-	-	-	-
SPP*TRT	PSME	cean	0.0000	-	-	-	-
SPP*TRT	PSME	manz	0.0000	-	-	-	-
SPP*TRT	PSME	none	0.0000	-	-	-	-