Does Elevated Temperature and Doubled CO$_2$ Increase Growth of Three Potentially Invasive Plants?

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Climate change, comprising an increase in carbon dioxide levels coupled with elevated temperature, may favor invasive plants, as they possess traits that will facilitate adaptation to a new climate. In particular, alien plants of subtropical origin introduced to a colder region are expected to increase the number and size of their populations and spread farther with climate change. Seedlings of three such woody alien species in New Zealand (*Archontophoenix cunninghamiana*, *Psidium guajava*, and *Schefflera actinophylla*) were grown in environmental chambers under the combination of two temperature (23.7 and 26 C [74.7 and 78.8 F]) and two CO$_2$ (450 and 900 ppmv) regimes, simulating current conditions and conditions projected for the end of the century. Total biomass of *S. actinophylla* was 45% higher and total leaf area 35% larger under doubled CO$_2$ compared to current CO$_2$. Root : shoot ratio was higher under doubled CO$_2$ across all species, and the number of branches was increased for *P. guajava*. The only significant interactive effect of elevated temperature and doubled CO$_2$ was for relative growth rate of the height of *S. actinophylla* seedlings. This study provides strong evidence of more vigorous growth of *S. actinophylla* under future conditions, particularly increased CO$_2$, whereas the other two species appear likely to maintain current growth rates. Better knowledge of the types of future conditions that may benefit such species, together with results of species distribution models and competition and eco-physiology studies will ensure robust weed risk assessments.

Nomenclature: Bangalow palm, *Archontophoenix cunninghamiana* (H. Wendl.) H. Wendl. & Drude; common guava, *Psidium guajava* L.; Queensland umbrella tree, *Schefflera actinophylla* (Endl.) Harms.

Key words: Alien plants, carbon dioxide, climate change, environmental chamber, naturalized plants.

Carbon dioxide levels and temperature are two of the major factors affecting plant growth, development and function (Morison and Lawlor 1999). Principally, increasing temperature enhances rates of plant development up to a temperature optimum, above which rates decrease again (Trudgill et al. 2005). Elevated CO$_2$ is expected to increase productivity of C3 plants by stimulating photosynthesis and inhibiting respiration (Rogers et al. 1994). Moreover, plants respond to elevated CO$_2$ by reducing stomatal conductance, which results in a reduced transpiration rate and an increase in the plant's water use efficiency (Drake et al. 1997). However, acclimation of photosynthesis to elevated CO$_2$ may occur, particularly if other factors such as low nutrient availability are limiting plant growth

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(Drake et al. 1997). Climate change effects on water use efficiency at the ecosystem level cannot simply be upscaled from responses at the plant level (Niu et al. 2011).

Global atmospheric concentrations of CO$_2$ and other greenhouse gases are increasing rapidly as a result of human activities, which in turn increase global average air and ocean temperatures (IPCC 2007). Indeed, CO$_2$ levels are projected to increase to between 730 and 1,020 ppmv by the end of the century (IPCC 2007). Observations from recent years have shown that the rise in CO$_2$ levels and temperature is consistent with projections from IPCC reports (Rahmstorf et al. 2007, 2012). A survey of 60 plant growth experiments conducted in both chamber and natural environments showed increased photosynthetic rates of, on average, 58% higher under elevated CO$_2$ compared to ambient CO$_2$ conditions (Drake et al. 1997). Across a range of scenarios, temperature is projected to increase globally on average by 1.1 to 6.4 C (34.0 to 43.5 F) by the end of the century (IPCC 2007). Already, plants have been affected by the temperature increase of 0.74 C globally over the last century (IPCC 2007), with evidence

Management Implications

Archontophoenix cunninghamiana, *Psidium guajava*, and *Schefflera actinophylla* are popular ornamental alien woody plants in New Zealand and elsewhere. Such plants from subtropical and tropical origin may benefit from climate change, naturalize, and become invasive in more temperate regions once climatic constraints in colder climates are removed. Responses to climate change, such as rising temperatures and CO_2 levels appear to vary, even within a single vegetation type such as woody plants. Of the three subtropical species in this study, *S. actinophylla* grew more vigorously under doubled CO_2 levels, resulting in increased biomass and leaf area. It also grew taller under the combination of doubled CO_2 and elevated temperature. Growth rates of the other two species did not differ under elevated temperature and doubled CO_2 compared to current levels. Consequently, climate change is likely to have a neutral or positive effect on growth of these three alien species. Although *S. actinophylla* is at a very early stage of invasion in New Zealand, early control of this species should be considered, due to its possible increase in performance under rising CO_2 levels. If co-occurring native species show negative growth responses to climate change, *A. cunninghamiana* and *P. guajava* may also have a competitive advantage, but this will have to be further assessed within a community context in another study. Woody alien species have been shown to be important invaders, and there are numerous subtropical plants introduced to temperate regions globally. This study highlights that such woody, bird-dispersed, subtropical species, which may benefit from climate change, should be screened as potential sleeper weeds.

of earlier occurrence of spring events in recent decades arising from a wide range of taxa and geographic locations (Walther 2004). Although many studies have investigated effects of temperature and CO_2 separately, in particular effects of CO_2 on crop plants of economic importance, there are still many uncertainties about the combined effects of elevated temperature and CO_2 on plant growth (Yoon et al. 2009). However, because changes in temperature and CO_2 are likely to occur simultaneously, it is of particular interest to study the interaction of these two factors (Morison and Lawlor 1999). It is expected that increasing temperature should increase responses to CO_2 (in C3 plants), because of the decreased ratio of photosynthesis to photorespiration and the decreased ratio of gross photosynthesis to dark respiration (Morison and Lawlor 1999). However, as indicated by the variable results of the temperature and CO_2 interaction on growth from different studies, biomass responses cannot be readily predicted from photosynthesis responses alone (Morison and Lawlor 1999).

Naturally, climate change will not affect all plant species to the same degree, with some individual species affected positively and others affected negatively (Thuiller et al. 2007). One group in particular that has been suggested to benefit from climate change is invasive plants. The projected change in abiotic conditions will provide opportunities for alien plants to expand into regions where previously they could not survive and reproduce (Walther

et al. 2009). Invasive plants may also possess traits that facilitate adaptation to the new climate: invasive plants often show rapid dispersal abilities (Dukes and Mooney 1999), they usually tolerate a wide range of climate conditions, and they often do not depend on coevolved pollinators or seed dispersers (Vilà et al. 2007). The question of how invasive plant species respond to rising CO_2 presents a research gap, requiring a case-by-case analysis (Hovenden and Williams 2010). Predicting correctly which invasive plants will benefit or suffer from elevated CO_2 could be of immense practical, economic, and strategic importance, informing decisions on weed management (Hovenden and Williams 2010). Elevated CO_2 has the potential to alter competition among and within species, leading to changes in structure and function of plant communities, which in turn will affect species at other trophic levels and even entire ecosystems (Hovenden and Williams 2010). Generally, it is expected that invasive plants, often being faster-growing species, may benefit more from elevated CO_2 (Thuiller et al. 2007). Greater response to elevated CO_2 has indeed been observed in alien compared to native congeners, studied mostly for forbs and grasses and some vines (Dukes and Mooney 1999; Song et al. 2010; Vilà et al. 2007, and references therein). Recent increases in CO_2, tested by growing plants in environmental chambers under CO_2 levels that existed at the beginning of the 20th century compared to current CO_2 levels, have already shown a far greater positive response to CO_2 in some invasive forbs than expected (Ziska 2003). However, it is difficult to separate species-specific effects from the group effects between native and invasive plants (Thuiller et al. 2007). Furthermore, little is known about the interactive effects of temperature and CO_2 on growth of invasive plants, and additionally, other limiting factors such as water, nutrient, and light availability may interact in complex ways.

Gaining better knowledge of how climate change will affect plant invasions is of critical importance, as alien plant invasions can drive native population declines (Baider and Florens 2011), with a recent meta-analysis of 1,041 field studies showing that alien plants significantly reduced the fitness of resident plant species by 41.7%, growth by 22.1%, species abundance by 43.5%, and diversity by 50.7% (Vilà et al. 2011). Invasive plants are a particular concern in New Zealand, with 92% of the ca. 26,500 vascular plant species being introduced (Lee et al. 2000). It can be expected that with a change in climate, species originating from warmer areas will be able to increase their populations and also colonize new areas (Walther et al. 2009). In particular, this may be the case for subtropical or tropical alien plants currently occurring in northern New Zealand only, that is, the warmest region of the country (with a mean annual temperature of 14 to 16 C; latitude of 35 to 37°S).

This is one of few studies to investigate the combination of elevated temperature and CO_2 on invasive plants, and particularly on woody species as they are rapidly increasing in importance as major invaders globally (Richardson and Rejmánek 2011). The study species are three newly naturalized plant species in northern New Zealand—bangalow palm, *Archontophoenix cunninghamiana* (H. Wendl.) H. Wendl. & Drude; common guava, *Psidium guajava* L.; and Queensland umbrella tree, *Schefflera actinophylla* (Endl.) Harms—which, like many alien plants, currently have limited geographic spread and small populations (Lee et al. 2000). However, we would expect an increase in their population size and a spread farther poleward with climate change, as has been projected by species distribution models (Sheppard 2013). Seedlings of the three species were grown in environmental chambers, simulating current temperature and CO_2 levels and conditions expected by the end of the century. Our aim was to investigate if these three species grow more vigorously under elevated temperature, under doubled CO_2, or under a combination of these two conditions, and we hypothesized that doubled CO_2 would have a stronger effect in combination with elevated temperature.

Materials and Methods

Study Species. Three newly naturalized alien plants in New Zealand were selected as study species: *A. cunninghamiana*, *P. guajava*, and *S. actinophylla*. All three species were chosen primarily because they originate from warmer tropical or subtropical native ranges and although currently limited to the northern part of the North Island, they have the potential to expand their range widely with climate change (Sheppard 2013). The seedling life stage is of interest in this study, as growth and survival at this early life stage are critical for the success of an invasion. Two of the selected species are shade-tolerant (*A. cunninghamiana* and *S. actinophylla*), which allows seedlings of such alien plants to invade undisturbed forests (Martin et al. 2009). The selected species are not dispersal-limited as they are both bird-dispersed, and thus able to spread over wide areas (Williams 2006), and are sold widely in plant nurseries in New Zealand. Availability of plants in nurseries is an important factor influencing invasiveness, with greater availability in nurseries and lower seed prices increasing invasion success of alien plants (Dehnen-Schmutz et al. 2007). *Archontophoenix cunninghamiana* of the family Arecaceae is a native of eastern Australia, and has been shown to be invasive in the Atlantic forest in Brazil (Christianini 2006). *Psidium guajava* of the family Myrtaceae is a native of Central America. It has been introduced to most subtropical and tropical regions because of its edible fruit, and has become invasive in many countries (U.S. Forest Service 2007). *Schefflera actinophylla*

Table 1. Experimental design across four time periods and three environmental chamber units. Future conditions are highlighted in bold.

	Chamber 1[a]	Chamber 2	Chamber 3
Period 1	T 1 CO_2 1	**T 2** CO_2 1	T 1 **CO_2 2**
Period 2	**T 2** CO_2 1	T 1 **CO_2 2**	**T 2 CO_2 2**
Period 3	T 1 **CO_2 2**	**T 2 CO_2 2**	T 1 CO_2 1
Period 4	**T 2 CO_2 2**	T 1 CO_2 1	**T 2** CO_2 1

[a] Abbreviations: T, temperature; T 1/CO_2 1, ambient/current values; T 2/CO_2 2, elevated/doubled values.

of the family Araliaceae is native to eastern Queensland and the Northern Territory in Australia (but also introduced to more southern regions of the country) and New Guinea. This species can also grow as an epiphyte and is highly invasive in the Pacific Islands (U.S. Forest Service 2007). All three species are thought to be of concern as potential weeds in northern New Zealand, as they are listed in the Regional Pest Management Strategy as alien plants that need to be further researched (Auckland Regional Council 2007).

Experimental Design. The experiment was conducted in environmental chambers (Contherm CAT 610 RHS, Contherm Scientific Limited, Lower Hutt, New Zealand), with an inner space of 63 by 51 by 63 cm (25 by 20 by 25 in). Fully factorial combinations of four treatments, temperature (ambient or elevated) and CO_2 (current or double), were replicated three times. The chamber formed the experimental unit, as only one treatment combination could be assigned to any given chamber. As only three environmental chambers were available, treatments were applied over four periods of time, with the experiment conducted in a Youden Square design (Table 1). This design is similar to the Latin Squares commonly used in environmental chamber experiments (Langhans and Tibbitts 1997), but having at least one missing column. In this case, time periods comprise a complete representation of all four treatments (i.e., a complete block design for the time period component design) and treatment combinations were balanced with respect to chambers (i.e., a balanced incomplete block design for the environmental chamber component design). The experiment was conducted from August 2010 to August 2011, each time period lasting 10 wk.

Ambient temperature level was chosen to simulate Auckland's current February (i.e., austral summer) temperatures. A diurnal cycle was applied with 16 h daytime and 8 h nighttime. Daytime temperature was set at 23.7 C, nighttime at 15.8 C (mean daily maximum/minimum temperature in February, measured at the Auckland Owairaka station 36.900°S, 174.733°E at 41 m [135 ft]

above sea level, calculated from data over 25 yr in the 1971 to 2000 period; National Institute of Water and Atmospheric Research 2010). For the future scenario, temperatures of 26 and 18.1 C were chosen, simulating the average projected change across six scenarios of + 2.3 C for Auckland's summer temperatures by 2090 (Ministry for the Environment 2008).

Due to technical difficulties in lowering CO_2 in the environmental chambers below indoor ambient levels (usually ranging from 400 to 500 ppmv), CO_2 was set at 450 ppmv for the current scenario, which is somewhat above the 396 ppmv globally in March 2013 (National Oceanic and Atmospheric Administration 2013), and at a future doubled CO_2 scenario of 900 ppmv. This is a plausible scenario for late in the 21st century, as atmospheric CO_2 concentration estimates for 2100 were calculated by the Bern carbon cycle to be 836 ppmv; if simulated by coupled climate-carbon cycle models, the value ranges between 730 and 1,020 ppmv by 2100 (IPCC 2007).

Humidity was set at 78.3%, which is equal to the mean humidity in February at 9:00 A.M. at Auckland's Owairaka station (see above for climate station details). A light intensity of 120 $\mu E\ m^{-2}\ s^{-1}$ was chosen, using Philips Alto 18W cool white bulbs. Using a conversion factor of 4.57 this results in a photosynthetic photon flux of approximately 550 $\mu mol\ m^{-2}\ s^{-1}$ (Langhans and Tibbitts 1997), comparable to a cloudy day in the peak of summer in Auckland (C. Macinnis-Ng, personal communication).

Typical fluctuations of the set parameters as indicated by Contherm are $\pm$ 0.3 C for temperature, $\pm$ 5% for humidity and $\pm$ 30 ppmv for CO_2. To measure accuracy, these parameters were monitored throughout the course of the experiment every 10 min with an integrated PLCS5 microprocessor control unit (Contherm Scientific Limited). Temperature was measured by a solid-state temperature sensor, humidity by a capacitive sensor probe, and CO_2 by an infrared detector (Contherm Scientific Limited). The data log showed that all mean values of temperature, humidity, and CO_2 were within the typical fluctuations indicated by the manufacturer. Although there were significant differences in humidity among the chambers during each time period, all means for the experimental periods were between 77.8 and 78.2%. There were significant differences among chambers in temperature, although fluctuations were also small (means ranging from 0.03 C lower to 0.07 C higher than the setting). Carbon dioxide fluctuated more, with means in each replicate differing between 6 and 20 ppmv amongst chambers. Technical issues (malfunctioning solenoids) during the first 3 wk of time period 1 meant that CO_2 cylinders were detached from chambers 1 and 2, resulting in ambient CO_2 concentrations of 450 to 550 ppmv (instead of the set 450 ppmv). Technical issues were

resolved and CO_2 levels were maintained as set for the final 7 wk of period 1.

For each time period, four seedlings of each of the three species (*A. cunninghamiana*, *P. guajava*, and *S. actinophylla*) were chosen randomly for each environmental chamber (12 seedlings per chamber, 48 across the whole experiment). Seedlings were obtained from North Island nurseries in Kerikeri, New Plymouth, and Ashurst. These seedlings were repotted a week before applying treatments, planting them into individual 1-L (34 oz) round plastic pots (12.5 cm diam by 10 cm height), with plastic saucers placed underneath. Pots were filled with Potpower™ potting mix (Debco, Melbourne, Australia). The 12 seedlings were positioned randomly within each environmental chamber for each time period. Seedling height ranged from 15 to 30 cm, and spacing between seedlings was around 13 cm, resulting in minimal shading from neighboring individuals. During the experiment a few plant insect pest infestations occurred, which were manually removed and thus controlled successfully soon after detection.

Pots were watered three times a week with 0.04 L (i.e., 3.25 mm [1.35 oz]) of water, accumulating to 42.25 mm a month, only two-thirds of the 65 mm rainfall usual for February. However, within the environmental chamber the plants were kept moist without water accumulating in the saucers underneath the pots.

Data Collection. For all plants, height was measured and the number of leaves counted at the beginning of the experiment and thereafter every 2 wk. Due to difficulties of measuring stem height of palm seedlings, height was defined as the distance from the soil to the leaf blade (i.e., stem plus petiole), choosing the leaf that maximizes this distance. For *S. actinophylla* the maximum distance from soil to petiole was chosen, and for *P. guajava* the distance from soil to the tip of the highest branch. For *P. guajava*, the number of branches was counted (counted as a new branch if it exceeded 3 cm). At the end of the experiment, root and shoot (stem and leaves separately) biomass was harvested and dried in the oven at 70 C for 48 h; dry mass was then determined. Total biomass as well as root : shoot ratio was additionally calculated. Leaf area for all species was measured by photocopying the removed leaves, weighing the extracted pieces of paper, and comparing to known paper mass. Specific leaf area (SLA) was determined by dividing leaf area by leaf mass.

Data Analysis. Data analysis was carried out using SAS statistical software (SAS Institute Inc., Cary NC, version 9.2 for Windows). Graphs were produced using R (R Development Core Team 2012, version 2.14.2 for Windows).

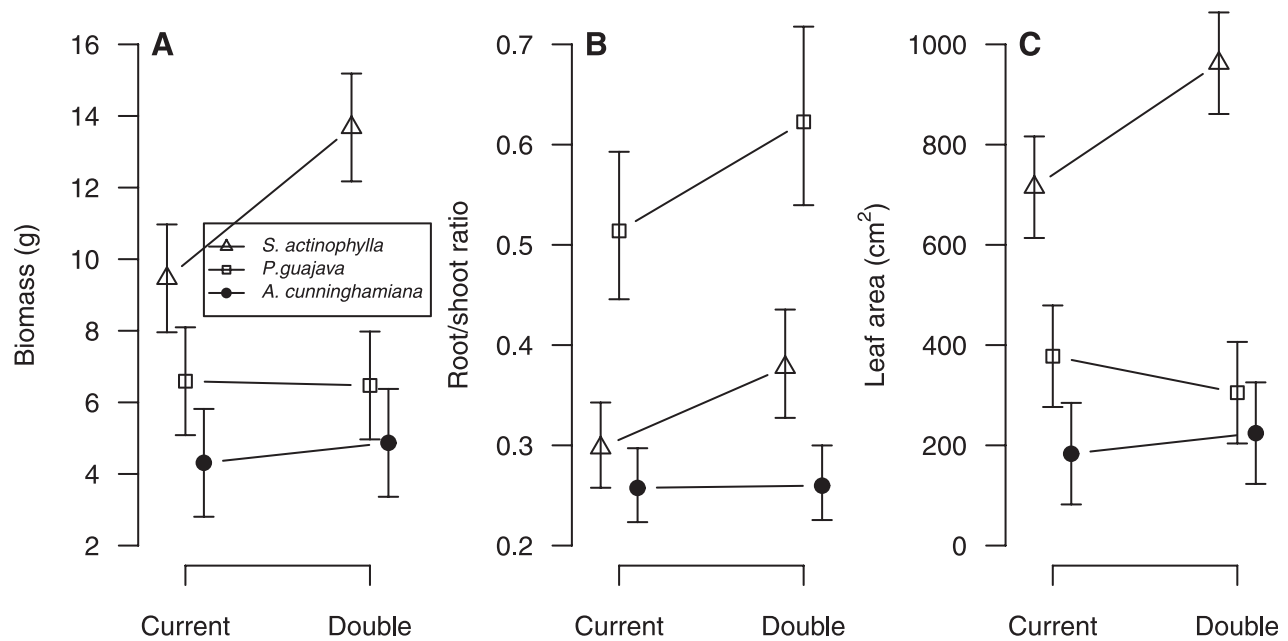As explained above, the environmental chamber formed the experimental unit, as only one of the four treatment

Figure 1. (A) Total biomass, (B) back-transformed root : shoot ratio, and (C) leaf area of the three species at current and doubled CO_2 levels; least squares means with 95% confidence intervals.

combinations could be assigned to a chamber at any given time. To achieve three replicates of each treatment combination, the experiment was conducted in four time periods using all three chambers during each period. Since environmental chambers and time periods were not in themselves of interest, these were regarded as block factors and therefore were treated as random effects. Destructive one-off measurement data such as biomass (root, shoot, and total), root : shoot ratio, leaf area, and SLA were analyzed by fitting a linear mixed model with temperature, CO_2, and species as the fixed effects. Restricted maximum likelihood (REML) was used to fit the linear mixed model to the data, because it gives more precise estimates of the means for balanced incomplete block designs. Type III hypothesis tests for the significance of each of the fixed effects and all two-way and three-way interactions were performed. Thereafter pair-wise comparisons of means were performed for those main effects and interactions that were found to be statistically significant ($P < 0.05$) in the type III hypothesis tests. The Tukey-Kramer method was used to adjust P values. The standard error of the difference between means is reported for all significant pair-wise comparisons. Means are referred to as least squares means (LSMs), that is, the average estimated values for the response variable at each level of selected factors, averaged over all the levels of the other factors. Root : shoot ratio and SLA were log-transformed before analysis; therefore the LSMs generated by the model were on the log scale. The difference between means was also converted back to its original units, giving the ratio between the two means, and the lower and upper 95% confidence limits around the ratio were calculated.

Assuming exponential growth, relative growth rates (RGRs) were estimated as the slope of a linear regression of natural log-transformed size vs. time (Paine et al. 2012). RGR was estimated for height, number of leaves, and number of branches (for *P. guajava* only). Slopes of these models were then analyzed in a similar manner to the biomass data mentioned above, using REML to fit the linear mixed model to the data, with temperature, CO_2, and species as fixed effects, and environmental chamber and time period as random effects. As different plants, both within and between species, entered the study with different basal sizes, the natural log-transformed baseline size (i.e., height, number of leaves, or number of branches at week 0) was fitted as a covariate in the model. Type III hypothesis tests for the significance of each of the fixed effects and all two- and three-way interactions were performed, and pair-wise comparisons of means for those effects found to be statistically significant.

Results and Discussion

Effects of CO_2 on Productivity. Elevated CO_2 resulted in more vigorous growth of *S. actinophylla*, whereas for *A. cunninghamiana* and *P. guajava* no significant effects of CO_2 were observed. In particular, pair-wise comparisons of biomass between CO_2 levels for each species separately showed that only for *S. actinophylla* was biomass significantly higher at doubled CO_2 levels compared to current CO_2 levels (Figure 1), with a difference between LSMs of 4.22 ± 0.83 g ($P < 0.001$), which is 45% higher total biomass (68% higher root and 37% higher shoot

Table 2. Type III tests of fixed effects for total biomass, log (root/shoot ratio), leaf area and log (SLA).[a]

Effect	Total biomass		Root : shoot ratio		Leaf area		SLA	
	F	P	F	P	F	P	F	P
T	0.06	0.803	0.11	0.752	0.55	0.458	0.01	0.941
CO_2	9.75	0.002**	7.03	0.042*	5.15	0.025*	0.37	0.581
Species	77.12	< 0.001***	84.79	< 0.001***	163.71	< 0.001***	1.19	0.308
T × CO_2	0.00	0.973	1.50	0.271	0.00	0.971	0.29	0.625
T × species	0.63	0.537	1.23	0.295	1.66	0.195	1.21	0.302
CO_2 × species	0.07	< 0.001***	1.98	0.142	9.66	< 0.001***	1.20	0.305
T × CO_2 × species	1.62	0.201	0.07	0.931	0.14	0.870	3.64	0.029*

[a] Abbreviations: SLA, specific leaf area; T, temperature.
* P < 0.05.
** P < 0.01.
*** P < 0.001.

biomass, data not shown) under doubled compared to current CO_2. Leaf area of *S. actinophylla* was 35% larger under doubled CO_2, with the difference between LSMs amounting to 247 ± 53 cm^2 (P < 0.001; Figure 1). There were no significant effects of temperature alone or the interaction between temperature and CO_2 on biomass or leaf area for any of the plant species (Table 2).

The results indicate that responses to increased CO_2 levels may be species-specific. In general, C3 trees are expected to do well: a review of free-air CO_2 enrichment (FACE) studies showed that, of the different functional groups of C3 plants, trees (mostly young, rapidly growing trees) experienced the highest increase in the light-saturated leaf photosynthetic rate (with an average of 47% compared to 31% across all functional groups) and the largest aboveground biomass production (with an average of 28% compared to 20% across all functional groups) (Ainsworth and Long 2005). However, Ziska (2003) suggested that the increase in CO_2 already experienced over the past century (from 284 to 380 ppmv) has had a significantly stronger effect on stimulating biomass of invasive plants than the CO_2 increase expected by the end of this century (from 380 to 719 ppmv in his study). Therefore, it is possible that growth of *A. cunninghamiana* and *P. guajava* compared to previous CO_2 levels of 284 ppmv may already have increased under CO_2 levels of 450 ppmv ("current" CO_2 treatment in the environmental chambers which, in addition, is already slightly higher than the actual current CO_2 level of 396 ppmv). In accordance with this, another study comparing two elevated CO_2 levels (500 and 650 ppmv) found a significant increase in growth of an invasive plant compared to current levels, but no difference between 500 and 650 ppmv (Hättenschwiler and Körner 2003), again suggesting that initial CO_2 increases are the most influential for stimulating plant growth.

Species-specific responses to increased CO_2 and climate change may lead to changes in community composition (Engel et al. 2009). If a fast-growing plant, such as *S. actinophylla,* increased its leaf area and thus cover in a natural environment, growth of other species may be suppressed, resulting in more asymmetric competition among individuals (Engel et al. 2009; Kallarackal and Roby 2012). Although *S. actinophylla* is at a very early stage of its invasion in New Zealand, such species with large potential impacts should thus be scrutinized for management attention as a sleeper weed.

Effects of CO_2 on Biomass Allocation. There was a significant effect of CO_2 on root : shoot ratio (Table 2), with root : shoot ratio at doubled CO_2 levels being 1.16 (95% confidence interval 1.04 to 1.29, P = 0.042) larger than at current levels (i.e., the species invested more in root biomass compared to shoot biomass at doubled CO_2 levels; Figure 1). Other studies have also shown that belowground biomass showed the strongest relative increase to higher CO_2 averaged over six herbaceous invasive species in the United States (Ziska 2003), for wild oat (O'Donnell and Adkins 2001), and for crop species such as potato (Fleisher et al. 2008). This might aid the plants in taking up more nutrients than they would be able to at ambient CO_2 (Luo et al. 2006; Rogers et al. 1996).

SLA was not affected by temperature, CO_2, or their interaction (Table 2). However, *P. guajava* had significantly more branches under doubled compared to current CO_2 (Figure 2; Table 3), with an estimated RGR of 0.155 wk^{-1} under doubled CO_2 compared to 0.121 wk^{-1} under current CO_2. This suggests that varying levels of CO_2 may result in different plant morphologies such as, in this case, decreased dominance of apical buds in favor of growth at lateral buds when light was not a limiting factor. Another study showed that elevated CO_2 increased branching and suppressed apical dominance in *Pinus radiata* D. Don seedlings (Conroy et al. 1990). Generally
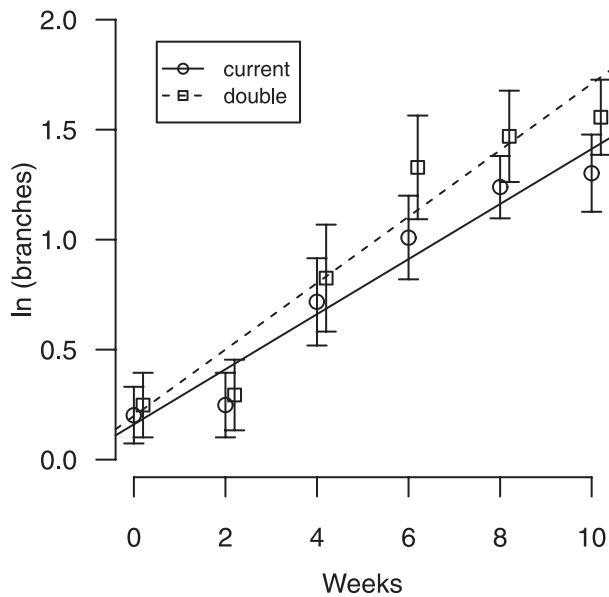
Figure 2. Number of branches of *Psidium guajava* at current and doubled CO_2 levels over 10 wk; least squares means with 95% confidence intervals, with slopes indicating estimated relative growth rate.

branching has not been reported widely, but a review of six species studied in FACE experiments showed an average increase in branching of 25% under elevated CO_2 (Ainsworth and Long 2005).

Effects of CO_2 and Temperature on RGR. There were no significant effects of CO_2 or the interaction of CO_2 and temperature on RGR of number of leaves (Table 3; Figure 3). For RGR of height, effects of temperature and

CO_2 differed depending on species (Table 3; Figure 3). However, the only significant difference between treatments was for *S. actinophylla*, with RGR of height under the combination of elevated temperature with doubled CO_2 treatment being higher than under the ambient, current treatment (with a difference in RGR of 0.024 cm cm^{-1} wk^{-1}; P = 0.013). Additionally, there was a strong trend for the elevated temperature with current CO_2 treatment having higher RGR than the ambient, current treatment (with a difference in RGR of 0.021 cm cm^{-1} wk^{-1}; P = 0.058).

In theory, the increase in photosynthesis is expected to be greater when the enzyme Rubisco is limiting at high temperature, because the rate of carboxylation at Rubisco is increased and the oxygenation reaction is competitively inhibited, decreasing photorespiration (Long et al. 2004). Indeed, a review of FACE studies showed that across experiments, photosynthesis was stimulated more at higher compared to lower temperatures (Ainsworth and Long 2005). However, predictions based on the understanding of the physiology do not necessarily correspond with observations of growth rates (Morison and Lawlor 1999; Williams et al. 2007). Similar to RGR of height of *S. actinophylla*, another study showed that even when finding a significant interactive effect of temperature and CO_2 such as in the case of a native and invasive C3 grass, the increase in growth was less than expected based on the sum of independently manipulated temperature and CO_2 treatments (Hely and Roxburgh 2005). The lack of interactive effects on biomass or RGR of any of the other species may also be due to the generally small effects of temperature in this study. Recent studies that found significant effects of temperature often used a higher increase in temperature for

Table 3. Type III tests of fixed effects for estimated relative growth rates of height, number of leaves, and number of branches of *Psidium guajava*.

Effect	DF[a]	Height			Leaves			Branches *P. guajava*		
		Den DF	F	P	Den DF	F	P	Den DF	F	P
Basal size[b]	1	129	22.63	< 0.001***	130	19.73	< 0.001***	42.3	45.25	< 0.001***
T	1	128	4.96	0.028*	130	0.11	0.744	42.4	0.01	0.925
CO_2	1	128	2.14	0.146	130	0.59	0.446	42.5	5.50	0.024*
Species	2	127	38.01	< 0.001***	129	19.23	< 0.001***			
T × CO_2	1	128	0.24	0.626	129	0.16	0.688	42.5	1.65	0.207
T × species	2	126	4.67	0.011*	128	3.75	0.026*			
CO_2 × species	2	126	2.06	0.132	128	0.64	0.528			
T × CO_2 × species	2	126	3.07	0.049*	128	0.23	0.797			

[a] Abbreviations: DF, numerator degrees of freedom; Den DF, denominator degrees of freedom; T, temperature.

[b] Basal size refers to basal height, number of leaves, or number of branches at the start of experiment.
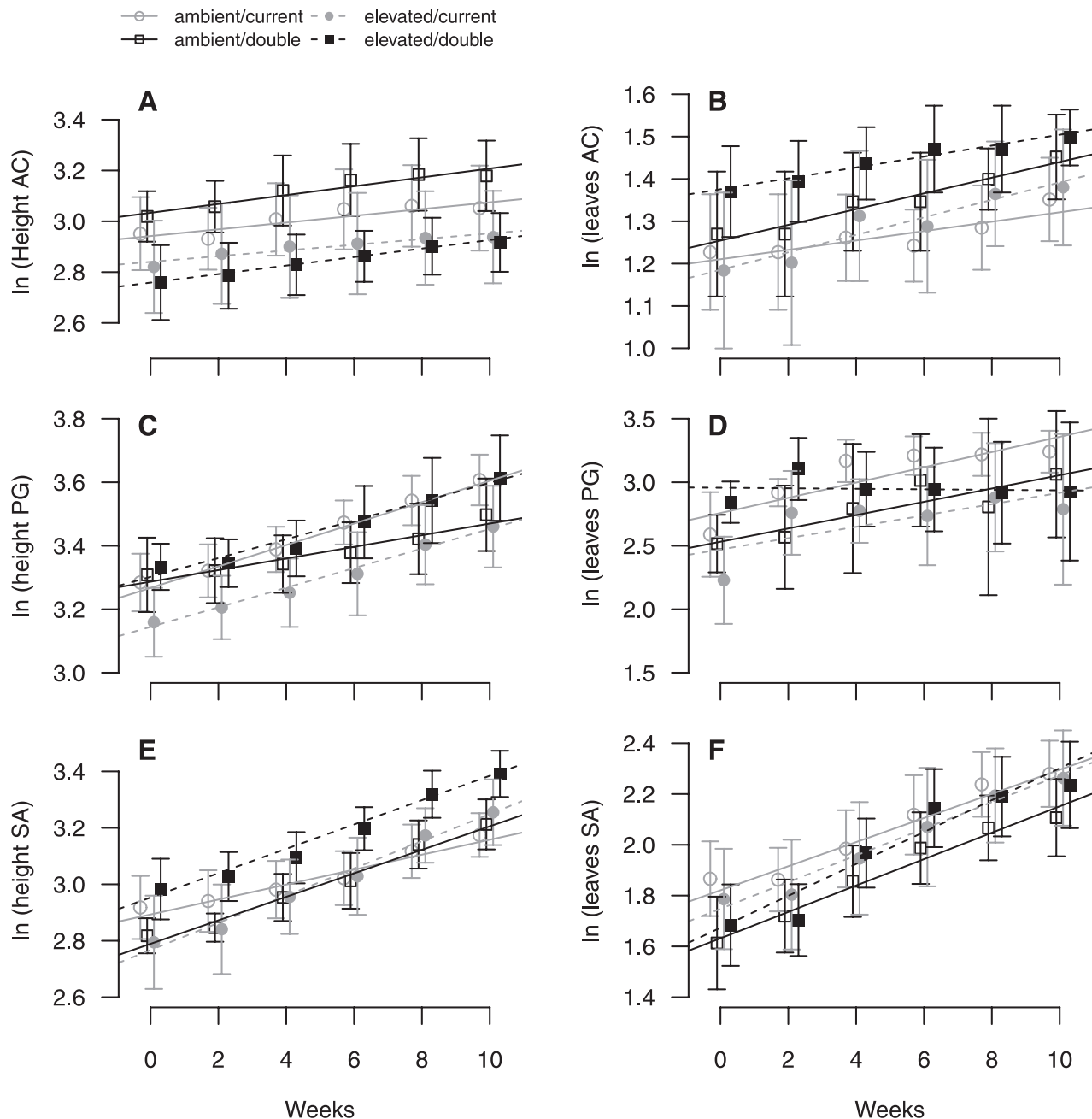
* P < 0.05.

** P < 0.01.

*** P < 0.001.

Figure 3. Height (left column) and number of leaves (right column) shown for the four treatment combinations over 10 wk; least squares means with 95% confidence intervals, with slopes indicating estimated relative growth rate. (A and B) *Archontophoenix cunninghamiana* (AC), (C and D) *Psidium guajava* (PG), and (E and F) *Schefflera actinophylla* (SA).

their treatments, such as 3 to 4 C (Hely and Roxburgh 2005; Lee 2011; Verlinden and Nijs 2010), or even as much as 10 C (Yoon et al. 2009), whereas the 2.3 C used in this study is comparatively small but more applicable to the scenarios for New Zealand. We chose this increase to simulate the average projected temperature increase across six scenarios; however, if temperature increases prove to be at the upper end of the range of scenarios, this may benefit these alien plants to a greater extent. Furthermore, for

subtropical species to persist in colder climates, increases in minimum temperature and with it reduced frosts during winter will be more critical (Sutherst et al. 2007). A further study should investigate the effects of elevated minimum temperature on growth of these species.

Experimental Limitations. Although being able to study the influence of temperature and CO_2 in the controlled conditions of an environmental chamber is of great

advantage, these chambers have been criticized due to their technical limitations such as size restrictions and pot effects (Long et al. 2004). Responses of these species may vary in natural environments, and therefore, the results of this study should be interpreted in combination with results from field studies (using FACE, or open-top chambers, as an intermediate tool towards a more natural environment). Nevertheless, a review comparing FACE and chamber studies on the effect of elevated CO_2 on crops has shown that results are mostly consistent, with both types of studies showing increased light-saturated photosynthesis, decreased stomatal conductance, increased shoot and root growth, and decreased SLA (Kimball et al. 2002). However, the extent of reduction of stomatal conductance and enhancement of root relative to shoot growth differed; with both having a stronger effect in the FACE compared to chamber experiments (Kimball et al. 2002). Another comparative review across a larger range of species found that there were some quantitative differences, with a smaller average increase in light-saturated C3 photosynthesis in FACE studies than in chamber studies (Long et al. 2004). Average increase in productivity in FACE studies amounted to 20% compared to 30% in chamber studies (Long et al. 2004). In a natural environment there are fewer space limitations, which enables longer-term studies, and plants can be grown in natural soil with no restriction on rooting volume (Long et al. 2004). On the other hand, FACE experiments experience larger fluctuations in CO_2, which may underestimate responses (Gifford 2004, and references therein). In this study, as we were interested in individual responses of three species at the seedling stage, an experiment in an environmental chamber was appropriate. Based on our results, a further study should now test the generality of the growth advantage of *S. actinophylla* under elevated CO_2 in a field situation. In a community context, direct physiological responses to elevated temperature and CO_2 levels may be less important compared to responses to secondary effects on factors such as nitrogen availability or competition (Williams et al. 2007). For potential weeds, comparisons with co-occurring native species will be of particular interest: should the native species show comparatively weaker or negative responses, management of the alien species will be more imperative. For example, Verlinden and Nijs (2010) found that for 10 herbaceous plant pairs, alien plants on average showed no response to a 3 C warming, whereas native congeners showed reduced biomass, which could result in a competitive advantage of the alien species under climate change conditions.

This study provides strong evidence that *S. actinophylla* can grow more vigorously under increased CO_2 levels, at least when resources are not limited, and factors such as competition and herbivory are not present. Root : shoot ratio is increased under elevated CO_2 across all three species studied here, and branching is increased for *P.*

guajava. However, surprisingly, there are no other differences in growth of *P. guajava* and *A. cunninghamiana* comparing either temperature or CO_2 levels. The performance of other alien, subtropical, woody, bird-dispersed plants under climate change should be investigated in order to obtain robust generalizations and to enable predictions on the types of conditions that may benefit such species. These experiments, together with results from species distribution models and competition and eco-physiology studies, will ensure that risk assessments are based on robust analyses of plant performance and impact.

Acknowledgments

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