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Bushkiller (*Cayratia japonica*) Growth in Interspecific and Intraspecific Competition

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Bushkiller was evaluated under inter- and intraspecific competition. In experiment 1, bushkiller, trumpetcreeper, and wild grape were greenhouse-grown alone and in two or three species mixtures in pots. Of the three species, bushkiller grew the tallest and had the greatest final biomass when grown alone. When all three species were grown together, bushkiller grew over twice the height of trumpetcreeper, over three times the height of wild grape, and over four times the biomass of either competing species. Plots of height over time showed that competition did not affect bushkiller or wild grape growth rate, but trumpetcreeper growth was reduced when grown with bushkiller. In experiment 2, bushkiller was grown in cultures of one, two, and three plants per pot to determine intraspecific competition effects on growth. Final height of bushkiller was not affected by intraspecific competition; however, bushkiller biomass decreased with increasing competition.
Nomenclature: Bushkiller, *Cayratia japonica* (Thunb.) Gagnep.
Key words: Additive design, exotic invasive species, perennial vine, target–neighbor design, weed competition.

Bushkiller is a perennial vine in the Vitaceae family with an aggressive growth habit that climbs and shades surrounding vegetation. It is native to temperate, subtropical, and tropical forests in Southeast Asia, Japan, India, Malaysia, Australia, and Taiwan (Hsu and Kuoh 1999). Bushkiller is invasive in the United States where it was first reported in Texas in 1964 (Brown 1992). Since that time, bushkiller has also been documented in Louisiana, Mississippi, Alabama, and North Carolina (Hansen and Goertzen 2006; Krings and Richardson 2006; Shinners 1964; USDA-NRCS 2006).

Bushkiller has been observed overtopping trees in North Carolina in a manner similar to kudzu [*Pueraria montana* var. *lobata* (Willd.) Maesen & S. M. Almeida]. Native to Asia, kudzu is listed as a noxious weed in 10 states across the southeastern United States (USDA-NRCS 2006). It is estimated that 3 million ha of the southeastern United States is covered in kudzu and increasing at 50,000 ha yr^{-1} (Forseth and Innis 2004). Kudzu is often observed outcompeting native trees and shrubs along highways and forest edges. Edges between forest and nonforest habitats favor plants that are shade and often competition intolerant. About 44% of trees in the continental United States are estimated to be less than 90 m from an edge (McDonald and Urban 2006; Riitters et al. 2002). In the Piedmont forests of North Carolina, two drought-tolerant oak species [*Quercus stellata* (Wangenh) and *Quercus falcata* (Michx.)] and trumpetcreeper [*Campsis radicans* (L.) Seem.] are common edge species (McDonald and Urban 2006). Exotic species such as kudzu and bushkiller may overtop edge tree species, forming monocultures and decreasing biodiversity.

Competition is one of the main factors that structure plant communities; therefore relative competitive ability of a plant may be used to predict its abundance in a plant community (Fraser and Keddy 2005). Grime (1973) described the four consistent features of ‘‘competitive’’ species: tall stature, a growth form (usually a large densely branched rhizome or expanded tussock structure) that allows extensive and intensive exploitation of the environment above and below ground, a high maximum potential relative growth rate, and a tendency to deposit a dense layer of litter on the ground surface. Bushkiller has a tall stature (shoots have been observed to 15-m tall in Charlotte, NC) and densely branched roots/rhizomes (A. West, personal observations). Phenotypic plasticity is another key characteristic of an invasive plant species and its ability to outcompete other plants (Burns and Winn 2006). Bushkiller inhabits a wide range of environmental conditions in its native range, from some of the wettest regions in the world to arid grasslands, and regions where winter temperatures drop to −7 C (USDA-ARS 2008).

Interspecific competition involves two or more plant species, and the magnitude of competition at the individual level can be quantified as the per-unit effect of individuals of neighboring species on the response of some target species, where response is a given measure of plant fitness (Firbank and Watkinson 1985; Goldberg 1996; Harper 1977). Intraspecific competition involves one species, and can be quantified as the per-unit effect of individuals of that species on the response of other individuals of the same species (Firbank and Watkinson 1985; Goldberg 1996; Harper 1977).

The simple additive approach is one method of demonstrating competition in plants (Connolly et al. 2001; Cousens 1991; Firbank and Watkinson 1985; Freckleton and Watkinson 2000; Gibson et al. 1999). This design compares plants grown ‘‘with’’ and ‘‘without’’ competition. Mixtures in the additive approach typically consist of a fixed, 1 : 1 ratio of two species; however, some studies are difficult to classify as simple, diallel, or additive in design (Freckleton and Watkinson 2000). Some of the problems associated with the additive design, such as the confounding effects of species proportion and density, are resolved using the target–neighbor design (Cousens 1991; Firbank and Watkinson 1985; Freckleton and Watkinson 2000; Gibson et al. 1999). This involves growing an individual of a ‘‘target species’’ with varying abundances of ‘‘neighbors’’ (either associate species or itself) (Cousens 1991; Firbank and Watkinson 1985; Freckleton and Watkinson 2000; Gibson et al. 1999).

Often, the per-unit biomass effect of neighbors on individuals of a target species is measured as the slope of a regression of target plant performance against the biomass of neighbors. To account for the dynamics of species interactions as they vary between the initiation and the completion of a competition experiment, numerous sequential measurements of each species per treatment are recorded (Connolly et al. 2001). Because of

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the climbing growth habit of the three perennial vine species in our experiment, it was determined that the destructive sampling method associated with weekly biomass measurements would not effectively demonstrate the effect of height on competition. Vine height can be a key determinate of relative competitive ability in fertile environments with dense canopy cover (Aerts 1999). Prolific vines are associated with structural disturbance in a plant community as they compete for light and overtop existing vegetation to create a new canopy layer (Aerts 1999; Forseth and Innis 2004). A comparison of the slopes of regression curves created from regularly collected height measurements yields a quantitative measure of the effect of neighboring species on height growth over time (Gibson et al. 1999; Goldberg and Landa 1991). Slopes of treatments with each species grown alone compared with each species grown in combination with one or both other species can be used to demonstrate the difference in height growth as influenced by interspecific competition.

We designed an experiment combining the simple additive approach with the target–neighbor design to determine interspecific competition between the exotic invasive bushkiller vine (target species) and two native vine species (neighbors), trumpetcreeper and wild grape (*Vitis* spp.). Trumpetcreeper and wild grape are important vines in southeastern U.S. forest communities. The nectar from trumpetcreeper flowers is one of the primary food sources for ruby-throated hummingbirds (*Archilochus colubris* Linnaeus) (Robinson et al. 1996) and wild grape provide food for a variety of birds and mammals. To address the effects of intraspecific competition on bushkiller growth, we conducted a second experiment in which bushkiller plants were grown at three densities.

Materials and Methods

To determine interspecific competition (experiment 1), root stock was obtained in June 2006. Bushkiller root stock was collected in Winston Salem, Forsyth County, NC and wild grape root stock was collected from Reedy Creek Field Lab, Raleigh, Wake County, NC. Trumpetcreeper root stock was purchased from a commercial source.[1] Each species was propagated from this root stock in a greenhouse and allowed to reach 30 cm in height. Plants were then transplanted into pots 30 cm in diameter with 25-cm depth. Wild grape root stock was planted 2 wk earlier than bushkiller and trumpetcreeper to increase size uniformity among species at the start of the experiment. This was done to reduce size bias, where one species may be judged as more competitive simply because it was the larger plant at the onset of the experiment.

Treatments included each species planted alone, all combinations of two different species, and all three species planted together. The density of bushkiller, trumpetcreeper, and wild grape in each treatment was held at one to preclude significant intraspecific interactions. Treatments with one species had one plant per pot, treatments with two species had two plants per pot, and treatments with three species had three plants per pot. Treatments were replicated three times and placed in randomized locations in the glasshouse with a total of 21 experimental pots. The first experiment was initiated June 26, 2007 and a repeat was initiated on October 12, 2007, with both conducted under ambient light.

To determine intraspecific competition (experiment 2), bushkiller root stock was collected and propagated as described for experiment 1. Treatments included one, two, or three bushkiller plants per pot. Treatments were replicated four times and placed in randomized locations in the greenhouse. The first experiment was initiated March 14, 2008 and a repeat was initiated on June 12, 2008. Pots in both experiments contained a commercial potting mix,[2] and one support structure was secured in the middle of each pot to serve as a climbing medium for the three vine species. Average daily temperature for the duration of both experiments was 32 C. Pots were watered twice daily and fertilized[3] once weekly.

In experiment 1, height measurements of the tallest shoot per species per pot were taken once a week for 6 wk. For analysis, 30 cm were subtracted from each measurement to account for height at trial initiation. At 6 wk after initiation (6 WAI), the number of inflorescences was counted for each species and all aboveground biomass was harvested and separated by species. The experiment was ended 6 WAI because bushkiller had reached the greenhouse ceiling. Plant biomass was oven dried at 50 C for 72 h for biomass determination. In experiment 2, height of tallest shoot per pot and number of leaves per plant were measured at 6 WAI. All plant aboveground biomass was harvested, separated by treatment, and oven dried as previously described for biomass determination. Dry weights were determined at the end of each trial as final biomass of a plant species depends on initial size and relative growth rate during the course of an experiment (Freckleton and Watkinson 2000; Gibson et al. 1999).

Data from both experiments were subjected to analysis of variance and means were separated using Fisher's Protected LSD ($P \leq 0.05$). Competition design in experiment 1 resulted in the following seven experimental treatments: bushkiller alone, trumpetcreeper alone, wild grape alone, bushkiller and trumpetcreeper together (BKTC), bushkiller and wild grape together (BKWG), trumpetcreeper and wild grape together (TCWG), and bushkiller, trumpetcreeper, and wild grape planted together (BKTCWG). These treatments resulted in nine statistical slope comparisons for analysis: bushkiller alone compared with BKTC, bushkiller alone compared with BKWG, bushkiller alone compared with BKTCWG, trumpetcreeper alone compared with BKTC, trumpetcreeper alone compared with TCWG, trumpetcreeper alone compared with BKTCWG, wild grape alone compared with BKWG, wild grape alone compared with TCWG, and wild grape alone compared with BKTCWG.

To analyze growth over time in experiment 1, a repeated-measures linear mixed model with time as an independent variable and treatment as a class variable was fitted (SAS Institute Inc. 2008). Both time and treatment were considered fixed effects. The model included a separate intercept and slope for each experimental treatment. Differences in the intercepts for the regression lines of growth over time represented treatment effects, whereas the separate fitted slopes represented treatment-by-time interaction. Type III tests of fixed effects were used for testing treatment (intercept) and time (slope) effects after all other effects were included in the model, i.e., significance of treatment slopes on time was tested conditionally on the observed intercepts and similarly when testing treatment effects (West et al. 2007). Pairwise comparisons of slopes between treatments were made using the ESTIMATE statement in SAS PROC MIXED. In experiment 1, linear regression curves of height growth on time ($y = y_0 + a_x T$) were modeled in SAS. In experiment 2, linear regression curves of final biomass and number of leaves

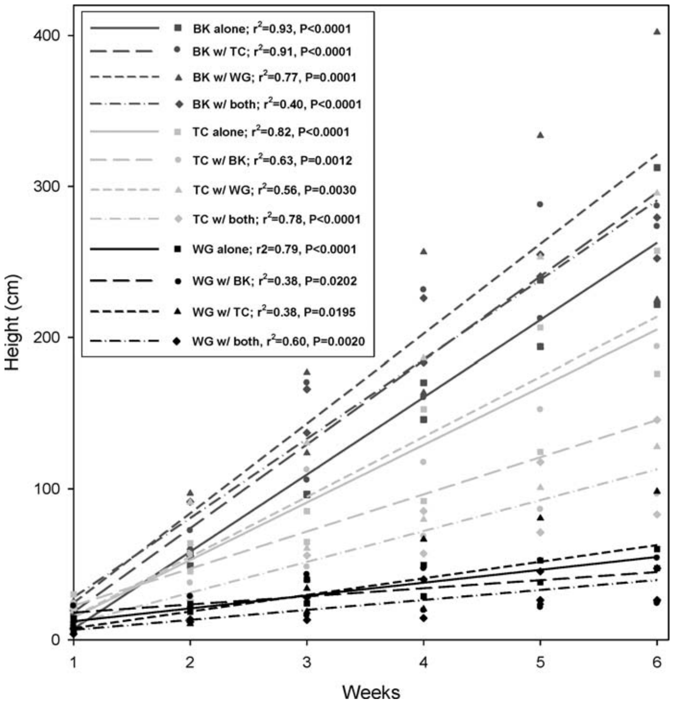

Figure 1. Rate of growth ($y = y_0 + a_xT$) for bushkiller, trumpetcreeper, and wild grape grown alone and in interspecific competition.

per plant ($y = y_0 + a_x$) were modeled in SAS. No treatment-by-repetition interactions were observed, therefore data were pooled by experiment.

Results and Discussion

Shoot elongation, represented by the magnitude of the slope of the regression curves, separated by species regardless of competition (Figure 1). When grown alone, the slope of bushkiller was 49.5 and greater than trumpetcreeper and wild grape at 38.1 and 8.7, respectively (Table 1). Rapid elongation rate is a trait common to invasive vines that make them structural parasites in a forest community (Forseth and Innis 2004). Slope estimates for bushkiller and wild grape elongation when in competition did not differ from their respective slopes when grown alone. However, the slope for trumpetcreeper was negatively affected when grown in competition with bushkiller or bushkiller and wild grape. No significant differences (P = 0.84) were found between intercepts for the separate regression lines.

The final heights of bushkiller, trumpetcreeper, and wild grape were 276, 217, and 54 cm, respectively, when grown alone (Table 2). Heights of bushkiller and wild grape plants grown alone were not different from those grown in competition. Trumpetcreeper was 102 cm shorter when grown with both bushkiller and wild grape than when grown alone. When bushkiller, trumpetcreeper, and wild grape were grown together, their final heights were 266, 114, and 37 cm, respectively. Bushkiller was the only species to produce inflorescences, and when in competition with trumpetcreeper the number produced was lower than when grown alone or with wild grape.

The average aboveground biomass of bushkiller grown alone was 221 g (Table 2). This value was 102 g greater than trumpetcreeper grown alone and 168 g greater than wild grape grown alone. Bushkiller biomass was reduced when grown with trumpetcreeper, but did not differ when grown with wild grape

Table 1. Slope estimates and slope comparisons of bushkiller, trumpetcreeper, and wild grape in the interspecific competition study.[a]

Species/pairwise comparison	Slope estimate	Slope comparison	P-value
Bushkiller alone	49.54 ± 5.24	—	—
Bushkiller with trumpetcreeper	53.06 ± 5.24	−3.52	NS
Bushkiller with wild grape	58.57 ± 5.24	−9.03	NS
Bushkiller with trumpetcreeper and wild grape	50.57 ± 5.24	−1.03	NS
Trumpetcreeper alone	38.14 ± 4.14	—	—
Trumpetcreeper with bushkiller	25.23 ± 5.85	12.91	0.029
Trumpetcreeper with wild grape	39.67 ± 5.85	−1.53	NS
Trumpetcreeper with bushkiller and wild grape	19.66 ± 5.85	18.48	0.002
Wild grape alone	8.73 ± 1.50	—	—
Wild grape with bushkiller	4.66 ± 1.50	4.07	NS
Wild grape with Trumpetcreeper	10.43 ± 2.12	−1.70	NS
Wild grape with bushkiller and Trumpetcreeper	6.31 ± 2.12	2.42	NS

[a] Slopes were compared via pairwise comparisons of the slope of each species in monoculture vs. its slope in competition with one or both other species. A significant P-value indicates that the growth rate of a species in monoculture differs from its growth rate in mixture. NS, not significant.

Table 2. Height, dry biomass, and inflorescence number of bushkiller, trumpetcreeper, and wild grape in the interspecific competition study at 6 wk after trial initiation.[a]

Treatment/species	Height	Dry biomass	Inflorescence
	cm	g	#
Bushkiller alone	267 ab	220.9 a	14 a
Bushkiller with trumpetcreeper	280 ab	170.6 b	9 b
Bushkiller with wild grape	313 a	205.5 ab	15 a
Bushkiller with trumpetcreeper and wild grape	266 ab	209.6 ab	9 b
Trumpetcreeper alone	216 bc	118.5 c	0 c
Trumpetcreeper with bushkiller	145 cd	15.3 d	0 c
Trumpetcreeper with wild grape	212 bc	93.3 c	0 c
Trumpetcreeper with bushkiller and wild grape	114 de	20.0 d	0 c
Wild grape alone	54 e	53.1 d	0 c
Wild grape with bushkiller	39 e	19.9 d	0 c
Wild grape with trumpetcreeper	62 de	36.0 d	0 c
Wild grape with bushkiller and trumpetcreeper	83 de	42.6 d	0 c

[a] Means within a column followed by the same letter are not significantly different according to Fisher's Protected LSD (P ≤ 0.05).

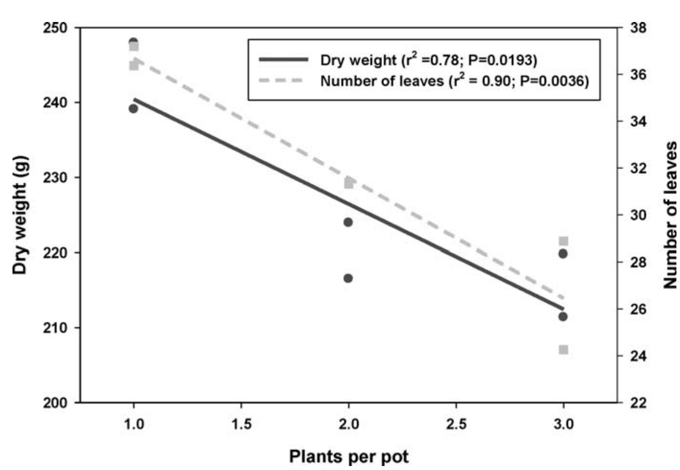

Figure 2. Dry weight at densities of 1, 2, and 3 bushkiller plants per pot and number of leaves per plant in intraspecific competition.

or both species. Trumpetcreeper biomass was 119 g grown alone, and this value dropped to 15 and 20 g when grown in competition with bushkiller or bushkiller and wild grape. Wild grape biomass was 20 to 53 g when grown alone or in competition, with no significant difference in these values.

In experiment 2, the mean final height of bushkiller was not significantly different when grown in treatments of one, two, or three plants and ranged from 306 to 314 g (data not presented). The final biomass, however, was 244 g for one plant, 220 g for two plants, and 216 g for three plants with a significant linear decrease (Figure 2). Likewise, the number of leaves per plant decreased in a linear fashion from 37 to 26.

The final height and biomass of bushkiller exceeded trumpetcreeper and wild grape whether grown alone or in competition. These differences may indicate bushkiller as the superior resource competitor. The increase in final height of bushkiller when grown with wild grape vs. bushkiller grown alone may indicate that neighboring vine species stimulate bushkiller elongation or serve as a ladder for bushkiller shoot support. Final shoot height and final biomass of trumpetcreeper was negatively affected when grown in competition with bushkiller or bushkiller and wild grape, but not when grown with wild grape. The effects of an exotic species on a native species and the effects of the native species competing with other native species are important comparisons when quantifying interspecific competition. If the exotic species is competitively superior to natives, it is expected to affect growth of native species more than coexisting natives (Vila and Weiner 2004). Wild grape was not affected by its coexisting native, trumpetcreeper, or vice versa; however, bushkiller negatively affected trumpetcreeper growth. This indicates that aggressive competition is absent between the two native species but bushkiller is the competitively superior species (Firbank and Watkinson 1985; Goldberg 1996; Harper 1977).

Intraspecific competition had no effect on bushkiller height; however, there was a difference in biomass and leaf number as affected by plant density. We conclude that this plant may thrive in monoculture, although per-plant biomass and leaf number may decrease as density increases. The interspecific competition experiment was conducted during the initial stages of plant development, with all plants starting at an average of 30 cm in height. The dynamics of the interactions between these species may change significantly over an extended period beyond the length of this experiment (Connolly et al. 2001). Since bushkiller accumulated two to four times the height or biomass of trumpetcreeper and wild grape in this 6-wk trial, the biological significance of this growth rate difference could increase over time as bushkiller accumulates photosynthate each year. In natural systems, the transition from primary to secondary succession in a forest results in changes to light quality, soil properties, soil–vegetation feedbacks, biomass accumulation, productivity, accumulation, and species composition (Guariguata and Ostertag 2001). The interspecific and intraspecific competition observed in this experiment indicate that the structural and functional properties of an ecosystem will be significantly altered to the detriment of native vine species (and others) when the exotic bushkiller vine is introduced.

Sources of Materials

[1] Gardens of the Blue Ridge, Pineola, NC.

[2] Metro Mix® 200; Sun Gro Horticulture, Bellevue, WA.

[3] Miracle-Gro® Water Soluble Lawn Food 36-6-6, The Scotts Company, Marysville, OH.

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