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Nutrient enrichment and soil conditions drive productivity in the large-statured invasive grass *Arundo donax*

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ABSTRACT

Introduction of the large-statured, invasive grass *Arundo donax* has negatively affected riparian ecosystems in Mediterranean-type climates and tropical regions worldwide. Control programs in large watersheds have been largely ineffective in reducing populations because of *Arundo*'s ability to recolonize after flooding and human induced changes to resource availability that facilitates growth. In a greenhouse study, we evaluated the relative effects of nitrogen, soil type, soil moisture, and light availability on *Arundo* growth. All treatments significantly influenced plant growth, but nitrogen addition and soils with organic materials had the strongest positive effect on above- and belowground biomass production. Ratios of above- to belowground growth were relatively stable across soil types and moisture levels, but allocation to belowground structures was significantly increased by nitrogen addition and full sunlight. Our results imply that control and management programs should address the human-altered nutrient and soil conditions associated with agricultural and urban watersheds that may facilitate dispersal, establishment, and growth of *Arundo* and other invasive plants.

1. Introduction

Invasive plants have disproportionately greater prevalence in riparian zones compared with upland terrestrial environments (Planty-Tabacchi et al., 1996; Stohlgren et al., 1998), and tend to have both larger populations and greater ecological impacts in these riparian ecosystems (Dudley and Collins, 1995). Large-statured, invasive grasses, in particular, can form extensive monocultures in rivers and associated wetlands, and often share characteristics that facilitate colonization and long-term dominance (Lambert et al., 2010a), including a primarily vegetative reproductive life history and a propensity to colonize disturbed systems with altered abiotic conditions (Saltonstall et al., 2010). Low elevation Mediterranean-type climate regions (surrounding the Mediterranean Sea, California, South Africa, Chile, and western Australia) tend to be associated with a high frequency of human colonization and plant invasions (di Castri, 1991; Vitousek et al., 1997), including associated riparian areas (Gasith and Resh, 1999; Hood and Naiman, 2000). Riparian systems in these regions are highly variable in seasonal discharge with scouring flows in winter rainy seasons and xeric conditions during the prolonged dry season. However, urbanization and agriculture in Mediterranean-type climate watersheds have resulted in altered flow regimes and enhanced nutrient inputs from these land uses (Zedler and Kercher, 2004; Juliet et al., 2007). These conditions are considered important factors in colonization by opportunistic species in terrestrial systems (Huenneke et al., 1990; Burke and Grime, 1996; Fenn et al., 1998) and coastal wetlands (Silliman and Bertness, 2004).

Arundo donax L. (giant reed; hereafter *Arundo*) is a large, perennial grass considered to originate from the Indian subcontinent (Polunin and Huxley, 1987), but recent evidence suggests a Mediterranean origin (Dudley et al., 2008). *Arundo* is now a noxious weed of Mediterranean-type climates and sub-tropical riparian ecosystems throughout the world (Lambert et al., 2010a). In coastal California landscapes and along the Rio Grande in Texas, *Arundo* forms monotypic stands, displaces native vegetation (Dudley, 2000), and reduces habitat suitability for native fauna (Herrera and Dudley, 2003; Kisner, 2004). Factors promoting *Arundo*'s invasiveness are not well studied, but the urbanization, nutrient pollution, and hydrologic alteration of streams and rivers that occur in Mediterranean-type climates may be major contributors (Gasith and Resh, 1999; Coffman, 2007). Direct analysis of the effects of altered resource conditions is critical to identifying the factors that contribute to the success of *Arundo* as has been done with other western North American riparian invaders such as tamarisk (Shafroth et al., 2005).

Agricultural and urban areas are often centered in the fertile flood plains of large rivers. Nutrient loading from these human systems into riparian corridors is assumed to be a key contributor to the success of *Arundo*. Coffman (2007) found a correlation between

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nutrient enrichment (primarily NO_3) from residential and agricultural land uses and *Arundo* abundance throughout coastal southern California watersheds. Other studies have shown that nitrogen addition increases *Arundo* above- and belowground biomass, as well as total yield (Angelini et al., 2005; Quinn et al., 2007). Quinn and Holt (2008) found that biotic and abiotic factors influenced the survival of *Arundo* rhizomes in field plantings and that soil interactions were key drivers of plant establishment. While several studies have demonstrated a relationship between nitrogen addition and *Arundo* biomass, it is unknown if growth response is dependent on the quantity of nitrogen introduced into the environment or whether other resource conditions that are often altered in human dominated riparian areas affect the growth dynamics of this invasive plant.

In this study, we evaluated the relative effects of multiple abiotic resource conditions on the growth of *Arundo* in a controlled environment. Our objective was to determine the extent to which various levels of nitrogen addition, soil type, soil moisture, and light affected *Arundo* above- and belowground growth. These variables are often altered in riparian corridors in agricultural and urban areas, but the relative importance of anthropogenic inputs and site specific characteristics on the invasive potential of non-native riparian plants remains unclear. Although phosphorus is often a limiting soil nutrient in Mediterranean-type climates (Day, 1983), there are naturally high levels in the young sedimentary geology of coastal California rivers where *Arundo* is invasive (Pettijohn, 1975). Therefore, we focused on nitrogen as a limiting nutrient. Treatment combinations and levels were selected to provide information about which resource inputs and habitats are most likely to promote *Arundo* growth and to provide information for site specific management under various environmental conditions.

2. Methods

2.1. Experimental design

We cultivated *Arundo* plants in a greenhouse at the University of California, Berkeley, and used a fractional factorial experiment that manipulated soil (substrate) type, nitrogen, soil moisture, and light. The experimental design consisted of 14 treatment combinations with 14 replicates each. Rather than a full factorial design, the treatment combinations emphasized various environmental conditions that were realistic and representative of riparian habitats in low-gradient floodplains in California and other Mediterranean-type climates (Table 1). This design also facilitated a direct analysis of main effects, one of the objectives of this study.

Arundo rhizomes were excavated in April from a study area on the Russian River, Healdsburg, California (coordinates: N 38.6074, W −122.8573). The standing culms were clipped, soil and debris removed, and the massive rhizomes cut into pieces of roughly similar size (163.0 ± 65.5 g wet wt; volume 156.0 ± 59.5 ml [mean ± one standard deviation]) and number of culm buds. Test rhizomes were held under cool, shaded conditions until planting (within 4–6 days), when one rhizome was placed into each 15 L plastic horticultural container (30 cm diameter; 28 cm height). Three soil types were used to simulate different riparian soils and were mixed using commercial landscape materials: a sand treatment consisting of washed coarse plaster sand, a silt treatment with low-organic content consisting of 50:50 mineral clay:fine sand mix by volume, and a riparian mixture composed of clay, sand, and a humus-based potting soil at a ratio of 2:2:1 by volume.

For the nitrogen (N) treatments, three levels of N availability (low N, high N, no N augmentation) were maintained to examine the effects of N input on *Arundo* growth. Nitrogen was applied to containers in the form of equal parts ammonium nitrate (NH_4NO_3) and potassium nitrate (KNO_3) at the rate of 10 g m^{-2} N added every three weeks (low N) or weekly (high N). These application rates created soil N abundances lower, but similar to other studies (Rickey and Anderson, 2004) and were roughly equivalent to inputs that might occur in riparian areas adjacent to upland agricultural uses in coastal California (Burton et al., 2007). Resulting nitrogen levels in the soil were likely variable among treatments owing to differential uptake by plants of different sizes and leaching rates of the various soil treatments.

Table 1
Treatment conditions used for growing *Arundo donax*. Treatment combinations were weighted to reflect the most common environmental conditions in riparian systems in California. Soil types were Riparian (mixture composed of clay, sand and a humus-based potting soil at a ratio of 2:2:1 by volume), Sand (washed coarse plaster sand), and Silt (50:50 v/v mineral clay–fine sand). Nitrogen treatments were no nitrogen added, equal parts ammonium nitrate (NH_4NO_3) and potassium nitrate (KNO_3) added to containers at the rate of 10 g m^{-2} N added every three weeks (low N), or weekly (high N). Soil moisture levels were water added only at leaf wilting (dry), soil kept moist (wet), or soil kept saturated. Plants were grown in either full sun or at 70–80% reduction in full sun using shade cloth. Treatments in bold are hypothesized to be the most common field conditions in coastal California riparian systems where *Arundo* is invasive and are used as controls.

Treatment #	Soil type	Nitrogen	Soil moisture	Light
1	Riparian	None	Wet	Sun
2	Riparian	Low	Wet	Sun
3	Riparian	High	Wet	Sun
4	Riparian	None	Wet	Shade
5	Riparian	High	Wet	Shade
6	Riparian	None	Dry	Shade
7	Riparian	None	Dry	Sun
8	Riparian	None	Saturated	Sun
9	Sand	None	Wet	Sun
10	Sand	High	Wet	Sun
11	Sand	None	Saturated	Sun
12	Sand	None	Dry	Sun
13	Silt	None	Dry	Sun
14	Silt	None	Saturated	Sun

Three soil moisture treatments were also established to simulate field conditions in riparian areas subject to *Arundo* infestation. These included (1) a saturated treatment, simulating near-stream environments that are perennially wetted, especially under regulated flow regimes or adjacent to irrigated farmlands; (2) a moist treatment such as might be found at a greater distance from a perennial stream, or in areas periodically wetted and then drying to moderate soil moistures as flows recede; and (3) a dry treatment as would be found on higher terraces or in channels that experience seasonal drought because of intermittent or altered flows. For the saturated treatment, each container was placed in a 20 cm deep pan which acted as a reservoir. Soil moisture treatments were maintained by hand-watering containers on the following schedules; either checked daily to ensure the presence of free water at the soil surface (saturated), watered every three to four days (twice weekly) to maintain soils near field capacity (moist), or only watered when soil moisture measured below 5% (dry) using a moisture probe (MP-917, Environmental Sensors, Inc.). When any plant in the dry treatment appeared to be in a wilting state, all plants in this treatment level were watered to prevent plants from experiencing excessive drought stress.

Finally, the light treatment consisted of plants either fully exposed to overhead sun in the glasshouse or shaded by commercial shade cloth attached to a wooden frame so that overhead and southern exposure was limited. This shade treatment resulted in 70–80% reduction of solar radiation, verified using a hand-held light meter (LI-1905 Quantum Sensor, LiCor Biosciences) on four occasions, including full sun and cloudy days. Treatment levels were similar to what would be experienced by plants establishing in a recently scoured river channel where all vegetation was removed or under a fully developed riparian canopy, for example under a