Abstract Although variation in the effectiveness of the plant-mycorrhizal association has been demonstrated among plant species and among crop cultivars, the level of specificity of the plant-mycorrhizal association in natural populations and, in particular, its effect on intraspecific plant interactions have not been explored. To examine the influence of the specificity of the plant-mycorrhizal association on intraspecific interactions in Allium vineale, we surrounded target plants with either genetically identical neighbors, neighbors from the same population, or neighbors from a different population, and planted them in pots either with or without a soil fungal community. Overall, the presence of a soil fungal community was beneficial for plant growth, and thus the soil fungal community effects in this system are dominated by the mutualistic effect of mycorrhizae. In addition, both the target plant and neighbor plants had a relatively greater benefit from the mycorrhizal association if the neighbors were genetically identical or from the same population than if the neighbors came from a different population. Thus, there is specificity in the interaction between A. vineale plants and the soil fungal community at the population level, and this specificity favors intraspecific interactions among plants from the same population. In addition, in the presence of the soil fungal community, the variance in plant size within a pot was greater among neighbors from a different population. Therefore the growth advantage for plants growing with neighbors from the same population was not due to pre-emption of resources by individual plants. This finding provides indirect evidence to support the hypothesis that plants from the same population were able to share a more efficient hyphal network.

Keywords Allium vineale · Arbuscular mycorrhizal fungi · Intraspecific interactions · Positive frequency-dependent feedback · Specificity

Introduction

Mycorrhizal fungi associate with approximately 80% of all plant species (Harley and Harley 1987; Smith and Read 1997), and can play an important role in P uptake (Bolan 1991; Koide 1991a). Although arbuscular mycorrhizal (AM) fungi are able to infect a broad range of host plant species (Harley and Smith 1983), the effectiveness of that interaction varies from both the mycorrhizal fungi and plant perspective. For example, from the fungal side, AM fungi can vary in sporulation rates on different host plants (e.g., Daft and Hogarth 1983; Hetrick and Bloom 1986; Sanders and Fitter 1992; Bever et al. 1996). From the plant perspective, plant species vary in mycorrhizal dependency (e.g., Hetrick et al. 1988, 1992; Koide and Li 1991; Wilson and Hartnett 1998), and there is variation in the effectiveness of specific AM fungal isolates on different plant species (e.g., Koomen et al. 1987; Dhillon 1992a). By using plants and fungal isolates from the same calcareous grassland community, Streitwolf-Engel et al. (1997) and Van der Heijden et al. (1998) have demonstrated that specificity in the plant-fungal interaction may be important in structuring natural plant communities. Variation in the effectiveness of the plant-mycorrhizal association has also been demonstrated within plant species, although these studies have been done primarily in agricultural systems using different crop cultivars (e.g., onion: Powell et al. 1982; pearl millet: Krishna et al. 1985; peas: Estaun et al. 1987; alfalfa: Lackie et al. 1988; wheatgrass: Di and Allen 1991; rice: Dhillon 1992b; barley: Boyechko and Tewari 1995). Although these studies have shown clearly that there can be considerable variation in the effectiveness of the
plant-mycorrhizae association within plant species, the effect of this variation on population dynamics and intraspecific interactions between plants in natural populations is unknown.

Mycorrhizal associations can alter the outcome of interspecific plant competition. Specifically, the presence of mycorrhizae can switch the competitive hierarchy among plant species that differ in their mycorrhizal dependency, such that strongly mycorrhizal-dependent plants outcompete less dependent or non-mycotrophic plants in the presence of mycorrhizae, but this competitive advantage disappears in the absence of mycorrhizal fungus (e.g., Fitter 1977; Hetrick et al. 1989; Hartnett et al. 1993; but see Koide and Li 1991). Mycorrhizae also have been demonstrated to influence intraspecific plant competition. In general, although mycorrhizae increase performance for all individuals at low densities, they amplify the intensity of intraspecific competition at higher densities (Koide 1991b; Allsopp and Stock 1992; Hartnett et al. 1993; Watkinson and Freckleton 1997; Facelli et al. 1999), as well as between juvenile and adult plants (Moora and Zobel 1996; Eissenstat and Newman 1990). The presence of mycorrhizae can also result in greater size or reproductive inequalities among competing individuals (Allsopp and Stock 1992; Shumway and Koide 1995; Facelli et al. 1999; but see Maffia and Janos 1993). These size inequalities may be due to pre-emption of resources by individuals with more effective mycorrhizal associations (Allsopp and Stock 1992; Shumway and Koide 1995; Facelli et al. 1999). Mycorrhizae have also been hypothesized to reduce size inequalities among neighbors, as the sharing of a mycorrhizal hyphal network could facilitate the transfer of resources among individuals (Shumway and Koide 1995; Grime et al. 1987). However, these studies did not test whether the effect of mycorrhizae on intraspecific interactions among plants was contingent upon the specificity in the plant-mycorrhizal association. We set out to examine this issue using asexual propagules from five genotypes of *Allium vineale*.

Previous field experiments have demonstrated that intraspecific competition in *A. vineale* is influenced by the genetic make-up of the neighboring plants, as plants with genetically similar neighbors outperformed those with genetically heterogeneous neighbors (Ronsheim 1996). The mechanism for facilitation among genetically similar neighbors in that study was unknown, but genotype-specific mutualistic interactions with mycorrhizae could potentially favor genetically similar neighbors, assuming that they are able to share a more effective hyphal network. This mechanism would require specificity among genotypes of *A. vineale* in their interactions with mycorrhizae. *A. vineale* has been shown to have positive feedback with the soil community (Bever et al. 1997), such that it grew better in soil previously conditioned by *A. vineale* plants. This positive feedback could potentially result in local co-adaptation between the plants and that soil community (Bever 1999), leading to the type of specificity necessary to favor interactions among genetically similar neighbors.

The following questions were addressed in this study: (1) Is there specificity in the plant-fungal association such that plants have a greater benefit when associated with the soil fungal community from their field of origin? (2) If so, does this specificity in the plant-fungal association affect intraspecific interactions among neighboring plants? Specificity at the genotype level could benefit genetically identical neighbors, although specificity at the level of the population could benefit plants growing with neighbors from the same population. (3) Does the presence of mycorrhizae decrease size inequalities among neighbors? One might predict less variance in size among genetically homogenous neighbors if they are able to share a more effective hyphal network, thereby reducing size inequalities among neighboring plants.

**Materials and methods**

**Study species**

*Allium vineale* L. (Liliaceae), wild garlic, is an introduced winter perennial commonly found along roadsides and in fields (Richens 1947). It emerges in early fall and grows until June, at which time its leaves and roots begin to die back and the bulb becomes dormant underground until the following fall. It produces an inflorescence in early summer that contains either flowers, asexual bulbils, or a combination of both. Seeds and bulbils ripen in early fall, and disperse a mean distance of 34 cm from the parent (Ronsheim 1994). Asexual bulbils range from 5 to 60 mg (mean mass 19.8 mg; Ronsheim 1996), and were used in planting this experiment. Offsets, a third propagule type, are underground asexual propagules analogous to the cloves of domesticated garlic. Plants can produce offsets during their first year, and the offsets were included as part of the total bulb mass in the analyses presented here. *A. vineale* plants also benefit from a facultative association with AM fungi (M.L. Ronsheim, unpublished data).

**Experimental design**

To test for specificity in the plant-mycorrhizal association and to determine whether the presence of the soil fungal community alters intraspecific interactions among neighboring *A. vineale* plants, target genotypes were planted in both non-mycorrhizal soil (fungicide treatment) and mycorrhizal soil (no fungicide) and with either genetically identical neighbors, neighbors from the same plant population, or neighbors from a different plant population, in a fully factorial design. This design allowed us to test for specificity on plant-mycorrhizal interactions both at the level of the genotype and the population, as well as to determine any effect of specificity on intraspecific interactions and size hierarchies among neighboring plants.

Asexual bulbils were collected in the summer of 1996 from the main study site at the Vassar Ecological Preserve and a second site approximately 1.25 km away. The five target genotypes were all collected from the main study site. Bulbils from each of five target genotypes were planted with either (a) two additional bulbils from the same target parent (genetically identical neighbor treatment), (b) one bulbil from each of two parents from the same field as the target genotype (same population neighbor treatment), or (c) one bulbil from each of two parents from the field 1.25 km from the main study site (different population neighbor treatment), for a total of three bulbils per pot (Fig. 1). Previous experiments have demonstrated that plants interact competitively at this density (M.L. Ronsheim, unpublished data). Although the specific neighbors planted with each target genotype were the same across soil treatments and replicates, different sets of parents were used as