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A faster inoculation assay for *Armillaria* using herbaceous plants

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Abstract

Armillaria (honey fungus) is a virulent necrotrophic pathogen that causes Armillaria root disease. Conventional *Armillaria* inoculation assays use young saplings as hosts and consequently are cumbersome, frequently conducted outdoors and take many years from establishment to analysis of infection. We have developed and evaluated a faster inoculation assay for *Armillaria* that uses herbaceous plants as hosts, is carried out in controlled conditions and reduces experimental durations to three months. Plant species of known susceptibility to *Armillaria* and comparisons between virulent *A. mellea* and opportunistic *A. gallica* were used to validate the assay. Mortality and diagnostic symptoms of *Armillaria* root disease such as epiphytic rhizomorphs and mycelial fans were used to assess levels of infection. We also attempted to reduce assay preparation time by substituting woody inocula

with agar inocula, but typical symptoms of Armillaria root disease were only observed on plants infected with woody inocula. Through our assay, we identified five new potential herbaceous hosts of *Armillaria*: *Kniphofia hirsuta, Hordeum vulgare, Lobelia cardinalis, Nicotiana tabacum* and *Helenium hoopesii* – further expanding the extensive list of plants with susceptibility to *Armillaria* and suggesting infection of herbaceous species may be more widespread than currently acknowledged.

Keywords: honey fungus; *Armillaria mellea*; infection; pathogenicity; root rot; Basidiomycete

1. Introduction

Armillaria (Basidiomycota; Physalacriaceae) is genus of approximately 40 described species of white rot pathogens that cause Armillaria root disease on hundreds of plant species (Baumgartner et al., 2011; Guillaumin and Legrand, 2013; Raabe, 1962; Royal Horticultural Society (RHS) Advisory Service, 2015). It is a global problem: in Canada, over 200 million hectares of forests are affected by Armillaria root disease (Chapman and Schellenberg, 2015; Cruickshank, 2011; Canadian Forestry Service, 2014), *Armillaria* infections are also reported from forests across Europe and North and South America (Brazee et al., 2012; Ferguson et al., 2003; Heinzelmann et al., 2012; Labbé et al., 2015) as well as commercial orchards and vineyards (Baumgartner, 2004; Elías-Román et al., 2013; Pellegrini et al., 2014; Schnabel et al., 2011) and Armillaria root disease is problematic in Africa, Asia and Australasia (Coetzee et al., 2015; Hood et al., 2015; Wingfield et al., 2009). Ornamental plants, including herbaceous species, are also affected (Blaedow et al., 2010; Coetzee et al., 2001; Travadon et al., 2012) and in the UK the majority of enquires received by the RHS Advisory Service over the past 19 years regarding plant diseases in UK gardens have been concerning *Armillaria* (RHS, 2015).

Armillaria root disease is caused primarily by the contact and subsequent colonisation of roots by rhizomorphs, which grow appressed to the surface of woody and fine roots and produce lateral branches that penetrate the root using a combination of mechanical and enzymatic processes, degrading both lignin and polysaccharides (Baumgartner et al., 2011; Mwenje and Ride, 1999; Snider, 1959; Thomas, 1934; Yafetto et al., 2009). Hyphae can also initiate infections, as can contact with infected roots (Mwenje et al., 1998; Rizzo et al., 1998; Solla et al., 2002). After successful root penetration, hyphae colonise the vascular and cambium tissue (Campbell, 1934; Thomas, 1934; Zeller, 1926) and cause aboveground symptoms that are suggestive of a reduced root system: wilting, chlorosis, leaf abscission, die-back and rapid onset of death. More specific signs of Armillaria root disease include internal mycelial fans, rhizomorphs attached to roots and fruiting bodies at the base of dead or dying trees (Baumgartner and Rizzo, 2002; Brazee and Wick, 2009; Guillaumin, 1977).

The serious ecological and economical damage caused by Armillaria root disease requires robust control mechanisms for this pathogen, but control of *Armillaria* is challenging, particularly because it can persist saprotrophically for decades after the host plant dies. This is a major problem in commercial forestry and agriculture when plantations, orchards and vineyards are established on recently cleared land and are subsequently infected from residual roots that remain in the soil from the diseased forest (Baumgartner and Rizzo, 2002; Leach, 1937; Labbé et al., 2015). Soil fumigants and chemical controls used to manage Armillaria root disease are expensive, sometimes ineffective and many are being phased out globally (Baumgartner et al., 2011; Percival et al., 2011; Thomidis and Exadaktylou, 2012; West and Fox, 2002), the use of traditional agronomic practices for Armillaria root disease management is usually labour-intensive and/or unsuccessful (Baumgartner, 2004; Chapman and Schellenberg, 2015; Cleary et al., 2013; Fox, 2003; Redfern, 1968), the availability and practicality of resistant cultivars is limited (Baumgartner

et al., 2013) and hitherto there is no biological control for *Armillaria* that has advanced beyond the experimental stage (Baumgartner and Warnock, 2006; Calvet et al., 2015; Hood et al., 2015; Pellegrini et al., 2014; Schnabel et al., 2011).

Artificial inoculation assays are a fundamental tool in developing effective control practices for plant pathogens; however, the conventional assays available for *Armillaria* use young saplings as host material, are generally laborious and are often conducted outdoors in uncontrolled conditions. Furthermore, the conventional assays are extremely slow: preparation of woody inocula usually takes three to six months, the host plants require years to establish prior to inoculation and then assessment of disease often lasts several years (Cleary et al., 2013; Morrison, 2004; Shaw et al., 1981; Solla et al., 2011). Inoculation assays using alternative hosts or other types of inocula such as rhizomorphs or wood chips (Holdenrieder, 1987; Pellegrini et al., 2014; Perez-Sierra and, Gorton, 2005) are not well-established and whilst the available *in vitro* assays are useful in that they are faster (Baumgartner et al., 2010; Baumgartner et al., 2013; Nogales et al., 2010), they involve the preparation of tissue cultured material and substantial microscopy and molecular work. For these reasons, a faster inoculation assay that could be conducted under controlled conditions, requires limited preparation and permits a simple assessment of infection would be desirable. As Armillaria root rot is generally regarded as a disease of woody species, *Armillaria* infection of herbaceous hosts has received little attention. Known herbaceous hosts are typically perennials or species that have succulent roots or tubers and have only been reported occasionally in the literature (Blaedow et al., 2010; Grasso et al., 2000; Guillaumin et al., 1993; Raabe, 1962; Robinson-Bax and Fox, 2002; Thormann et al., 2001). In this work, we attempt to alleviate some of the difficulties associated with the existing inoculation assays by (i) assessing the suitability of various herbaceous species for use as host plants in *Armillaria*

inoculation assays and (ii) determining whether agar can be used as a substitute for woody inocula to expedite inocula preparation time.

2. Material and Methods

2.1 Armillaria isolates and preparation of inocula

Isolates of *Armillaria mellea* (ELDO17 and CG440) and *Armillaria gallica* (ANA220) were routinely cultured on potato dextrose agar (PDA) at 25°C in the dark. Isolates were acquired from culture collections maintained at United States Department of Agriculture-Agricultural Research Service, Davis, USA and the Royal Horticultural Society, Wisley, UK and were initially identified by amplification of the IGS1 region and subsequent restriction digestion analysis using *Alu*I (Harrington and Wingfield, 1995) or by pairing with haploid tester isolates (Guillaumin et al., 1991). These isolates were selected as they have been previously utilised in experimental work (Beal et al., 2015; Ford et al., 2015) and represent a virulent species of *Armillaria* (*A. mellea*) and a more opportunistic species (*A. gallica*) (Gregory, 1985; Morrison, 2004; Rishbeth, 1982).

Agar inoculum consisted of three mycelial agar plugs excised from a PDA plate of a four-week *Armillaria* culture. Woody inoculum was prepared according to Perez-Sierra (2004). Briefly, billets measuring between 15 and 20 mm in diameter were removed from hazel (*Corylus avellana*) trees and cut into sections 10 cm in length. Billets were rinsed in water and then inserted into 500 ml wide mouth jars (VWR), covered with deionised water and autoclaved three times, removing and replenishing the water each time. The billets were dried and immersed in carrot agar (700 g carrot, homogenised and filtered, 20 g agar, 1 litre deionised water), inoculated using mycelial agar plugs from a four-week *Armillaria* culture and colonised at room temperature in the dark for six months prior to use.

2.2 Plant inoculations

Eleven herbaceous plants and one woody plant species were used in inoculation assays. Plants were selected on the basis that they were typical ornamental plants found in UK gardens or were model species, and include known *Armillaria* hosts and plants of undetermined susceptibility to *Armillaria* (Table 1). Plants were obtained as plugs and established in 9 cm diameter pots containing Sinclair Medium Grade Peat-Based Potting and Bedding Compost in growth rooms for one month prior to inoculation. Growth rooms used fluorescent lighting and photoperiods of 16 h light and 8 h darkness with temperatures between 15°C to 25°C.

Plants were inoculated with agar plugs of *A. mellea* (CG440 and ELDO17) and *A. gallica* (ANA220) and woody inocula of *A. mellea* (CG440) and *A. gallica* (ANA220) by inserting three mycelial agar plugs or two hazel billets 5 cm from the surface of the soil adjacent to the main root to maximise root contact. Control plants were mock-inoculated with sterile agar plugs or sterile hazel billets as appropriate. Due to the large number of plant species evaluated in this assay and the length of time required for this slow-growing fungus to produced infection symptoms, a minimal number of plants required for statistical purposes were inoculated: four replicate plants were used per treatment including the control, with the exception of *Fuchsia magellanica* and *Arabidopsis thaliana* where three replicate plants were used. Plants were organised using a randomised block design on growth room benches.

2.3 Analysis of infection

Three months post inoculation, plant height was measured and the number of stems, leaves and flowers was recorded when applicable dependent upon each plant species. Plants were then removed from their pots, soil was washed from the roots and the entire plant was weighed to measure wet weight. The plants were subsequently dried for two to three days in an oven at 70°C and reweighed to measure dry weight. The soil and inocula in each pot was inspected for presence of rhizomorphs and roots were examined prior to drying for presence of mycelial fans and epiphytic rhizomorphs. Viability of woody inoculum was determined by pealing back the bark of the hazel billets: viable inoculum had visible mycelial fans (Morrison, 2004). Plants that died throughout the experiment were examined for the presence of *Armillaria* to confirm likely cause of mortality. Mortality was also recorded at the end of the experiment. Data were analysed using one-way analysis of variance (ANOVA) and means were compared for significant main effects ($p \geq 0.05$) using Dunnett's post-hoc test in SPSS.

3. Results

3.1 Agar verses woody inocula

A total of 276 plants were inoculated with agar or woody inocula of *Armillaria* or were mock-inoculated with sterile agar plugs or hazel wood billets as appropriate in order to develop a faster inoculation assay for *Armillaria*. We investigated whether agar inocula could be used as an alternative to the woody inocula typically utilised in *Armillaria* inoculation assays. Plants were destructively analysed three months post inoculation and 93% of *A. mellea* (CG440) woody inocula and 98% of *A. gallica* (ANA220) woody inocula remained viable during the experimental period. Rhizomorphs were evident in the soil or

were observed emerging from the woody inocula in 52% and 24% of pots inoculated with woody inocula of *A. gallica* and *A. mellea*, respectively (Table 2). In contrast, recovery of agar inocula of either species from the soil was not possible and therefore viability of agar inocula was unable to be determined. No rhizomorphs were visible in the soil in pots inoculated with agar inocula. As expected, no rhizomorphs were observed in the soil of the mock-inoculated control pots. Diagnostic symptoms of *Armillaria* infection were present when plants were inoculated with woody inocula, but were not observed on plants inoculated with agar inocula, or on mock-inoculated control plants (Section 3.2). Infection assays using agar inocula of *A. mellea* and *A. gallica* were repeated twice in a larger experiment involving 23 plant taxa grown under similar conditions, but agar inocula could never be recovered, no rhizomorphs were observed and no diagnostic signs of *Armillaria* infection were apparent (data not shown).

3.2 Suitability of herbaceous plants for use in Armillaria inoculation assays

Eleven herbaceous and one woody plant species were evaluated to determine their suitability for use as host plants in *Armillaria* inoculation assays. Nine out of the twelve plant species inoculated with woody inocula of either *A. mellea* or *A. gallica* displayed signs of *Armillaria* infection such as the presence of mycelial fans and rhizomorphs firmly attached to roots causing necrotic lesions (Table 2). No symptoms of *Armillaria* infection were detected on *Arabidopsis thaliana*, *Erigeron speciosus* and hybrid *Geranium*. In total, rhizomorphs were observed attached to roots on 20% of the plants that were inoculated with woody inoculum of *A. gallica* and on 2% of the plants inoculated with woody inoculum of *A. mellea*. Internal mycelial fans were identified in 17% and 26% of plants inoculated with woody inocula of *A. gallica* and *A. mellea*, respectively (Figure 1).

Most plant species grew well initially but mortality was high in *E. speciosus* starting from four weeks post inoculation (30% after week four; 50% at the end of the experiment) across all groups including the non-inoculated controls. No epiphytic rhizomorphs or mycelial fans were detected in *E. speciosus*, indicating the cause of death was likely to be independent of *Armillaria* infection. Similarly, *Nicotiana tabacum* plants demonstrated reduced vigour, appeared chlorotic and suffered 25% mortality in total across all treatment groups by the end of the experimental period (Table 3). Thus, whilst epiphytic rhizomorphs were observed on one of the plants inoculated with woody inocula, it is not possible to attribute mortality to *Armillaria* infection in this case. In other species, such as *Chrysanthemum maximum, Fragaria* × *ananassa, Heuchera americana, Kniphofia hirsuta* and *Lobelia cardinalis,* mortality was only observed in the plants inoculated with woody inoculum of either *A. gallica* or *A. mellea*, and in 75% of these dead plants, internal mycelial fans were present or rhizomorphs were attached to roots causing necrosis. Epiphytic rhizomorphs were observed most frequently on *N. tabacum, Fuchsia magellanica, Helenium hoopesii* and *L. cardinalis* and mycelial fans were present most often on *Fragaria* × *ananassa, Hordeum vulgare* and *H. americana*. Mortality rates in plants inoculated with wood inocula of *A. mellea* and *A. gallica* were similar: 20% and 17%, respectively. Differences in plant growth parameters, with the exception of weight measurements for *C. maximum*, were non-significant (Table 4).

4. Discussion

Armillaria is often described as a pathogen of woody species, yet there are several reports of natural infections of herbaceous plants (Blaedow et al., 2010; Grasso et al., 2000; Thormann et al., 2001). Here, we have used herbaceous plants that are quick to establish and easy to manipulate as an alternative to woody species in long-term trials or use of *in vitro* approaches

that require laborious tissue culture methods. This assay can be completed in three months - a substantial reduction in experimental duration in comparison to traditional inoculation assays which may last for several years (Cleary et al., 2013; Mallett and Hiratsuka, 1988; Shaw et al., 1981; Tsopelas and Tjamos, 1997) and comparable with *in vitro* infection assays (Baumgartner et al., 2010; Baumgartner et al., 2013). Moreover, our assay is conducted in a controlled environment, which will avoid fluctuating environmental conditions that can introduce further variability to experiments and will also allow the use of transgenic strains - something that would be problematic in an open field trial.

An assay of this type is only useful if it correlates to established levels of pathogenicity and host resistance under typically tested conditions. In observations of natural infections and in pathogenicity assessments, *A. mellea* is shown to be a virulent and aggressive pathogen whereas *A. gallica* is generally regarded as opportunistic or saprotrophic (Gregory, 1985; Guillaumin et al., 1993; Morrison, 2004). Furthermore, *A. gallica* produces extensive networks of rhizomorphs in natural environments, whereas *A. mellea* rhizomorphs are rare in nature (Baumgartner and Rizzo, 2002; Guillaumin et al., 1993; Rishbeth, 1982; Tsykun et al., 2012). This is consistent with our observations, where *A. gallica* rhizomorphs were found more often than *A. mellea* rhizomorphs in pots inoculated with woody inocula and were more commonly attached to roots, yet *A. gallica* mycelial fans were less frequent than *A. mellea* mycelial fans in roots. This supports the notion that *A. gallica* is less virulent than *A. mellea*, because *A. gallica* is clearly able to contact and colonise plant roots, yet causes less damage to the host. Accordingly, it may have been anticipated that mortality would have been higher in plants inoculated with *A. mellea* than in plants inoculated with *A. gallica* (Rishbeth 1982), but this was not the case and mortality was broadly similar in plants inoculated with either species. It is possible that differences in mortality may be more apparent with longer experimental durations. We included several species with known

susceptibility to *Armillaria* in our assay, such as the woody host *F. magellanica*, to provide further validation of its utility (Raabe, 1962; RHS Advisory Service, 2015). As expected, epiphytic rhizomorphs and mycelial fans were present in the root system of 50% of *F. magellanica* plants inoculated with woody inocula of *A. mellea* and *A. gallica*. Similarly, *Armillaria* infection was observed in other known hosts: *C. maximum*, *Fragaria* × *ananassa* and *H. americana* when inoculated with the woody inocula.

Non-woody hosts have been used in *Armillaria* inoculation assays previously, but these mainly involve detached tubers of either potato (*Solanum tuberosum*) (Garrett, 1956; Gregory, 1985; Thomas, 1934) or cassava (*Manihot esculenta*) (Mwenje et al., 1998). Strawberry plants (*Fragaria* × *ananassa*) have also been used as hosts in longer experiments constructed outdoors or in glasshouses (Beal, 2013; Fox and Popoola, 1990; Pellegrini et al., 2014; Percival et al., 2011). Building on this previous work, and given the results of this assay where 50% infection levels and 25% mortality were observed in strawberry plants inoculated with woody inocula, strawberry seems a suitable host for use in small-scale inoculation assays such as this.

Five species, with no previous reports of susceptibility to *Armillaria*, were identified as potential new hosts during this work owing to the presence of epiphytic rhizomorphs and mycelial fans observed post inoculation: *H. vulgare, K. hirsuta, L. cardinalis, N. tabacum* and *H. hoopesii*. The latter four species have fleshy roots - often characteristic of plants susceptible to *Armillaria* infection. The ability of *Armillaria* to infect *H. vulgare* is interesting because generally meadow grasses, with the exception of the larger grasses such as *Arundinaria* and *Cortaderia* where incidents of Armillaria root disease have been reported occasionally, are not thought to be vulnerable to *Armillaria* infection (Fox, 2003; Hughes et al., 1996; Raabe, 1962; RHS Advisory Service, 2015), presumably due to the absence of

large roots and fleshy stems. *Hordeum vulgare* appeared to be tolerant to *Armillaria* infection, since 75% of plants inoculated with woody inocula were infected, but there was no mortality. This high tolerance of infection is probably the reason that *Armillaria* infections of *H. vulgare* or other meadow grasses have not been reported previously.

In our efforts to develop a faster inoculation assay for *Armillaria*, we attempted to measure plant growth parameters to indicate levels of infection; however, with the exception of one host, differences in plant growth parameters between plants inoculated with woody inocula and non-inoculated controls were non-significant, irrespective of visible *Armillaria* infection. Despite this, a general trend of a reduction in height, weight and foliage was observed in some species in plants inoculated with woody inocula in comparison to non-inoculated controls or plants inoculated with agar inocula. For example, a reduction in the number of leaves, wet weight and dry weight was evident in strawberry plants inoculated with woody inocula in comparison to non-inoculated control plants or plants inoculated with agar inocula. In other species however, there was limited correlation between levels of infection and mortality and plant growth parameters. This has been noted in other work, where there were no significant differences in plant weight or height between infected and non-infected plants (Baumgartner et al., 2010; Westwood et al., 2012), although other *Armillaria* pathogenicity studies have found significant differences in the number of flower spikes and dry weight (Calvet et al., 2015). The utility of growth parameters as way of assessing infection levels appears inconsistent for use in *Armillaria* inoculation assays.

We also attempted to reduce the time required for preparation of inocula by assessing whether woody inocula could be substituted with agar inocula, but agar inocula proved ineffective at establishing infections. Another recent study has also endeavoured to use agar as *Armillaria* inocula without success (Sitienei et al., 2015). Agar plugs have been used

previously in *Armillaria* inoculation assays, but only *in vitro* (Baumgartner et al., 2010; Baumgartner et al., 2013) or in the inoculation of cassava tubers where mycelial agar plugs were inserted into wounds that were subsequently sealed to prevent desiccation (Mwenje et al., 1998). Since desiccation of inocula is common in *Armillaria* inoculation assays, and smaller-sized inocula is more prone to drying out than larger inocula (Baumgartner et al., 2010; Perez-Sierra and Gorton, 2005), agar plugs seem inappropriate for use as soil inocula unless protected from desiccation.

As often observed in *Armillaria* inoculation assays (Baumgartner et al., 2010; Gregory, 1985), we had some plants that appeared to escape infection: hybrid *Geranium* (a known host) and *A. thaliana* and *E. speciosus* did not exhibit any Armillaria root disease symptoms. Inconsistent survival times and infectivity of *Armillaria* inoculum is often reported (Perez-Sierra and Gorton, 2005) and lack of infection is commonly attributed to this variability (Gregory, 1985). On the other hand, we observed infection when no rhizomorphs were visible in the inoculum or in the soil; again, this is consistent with other work (Gregory, 1985) and demonstrates the difficulties that *Armillaria* researchers face when attempting to ascertain infection levels in artificial inoculation assays. Nevertheless, this rapid inoculation assay will help to expedite screening plants for resistance to Armillaria root disease and assist in fast assessment of isolate virulence and in assaying control agents. The identification of five new potential hosts of *Armillaria* suggests that the susceptibility of herbaceous species to *Armillaria* infection may be overlooked and potential for infection should be considered when horticulturalists are making planting decisions in areas affected by Armillaria root disease.

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Table 1. Plant species used in inoculation assays

Plants	Vernacular name	Variety	*Armillaria* species known to infect plant	Reference
Arabidopsis thaliana	Thale cress	-	-	-
Chrysanthemum maximum	Chrysanthemum	Nanus	*A. mellea*	Guillaumin et al., (1993)
Erigeron speciosus	Aspen fleabane	Azure fairy	-	-
Fragaria × ananassa	Strawberry	Symphony	*A. mellea; A. gallica*	Fox and Popoola (1990); Raabe (1962)
Fuchsia magellanica	Hardy fuchsia	Tom thumb	*A. mellea sensu lato*	Raabe (1962)
Geranium [hybrid]	Geranium	Blue sunrise	*A. mellea sensu lato*	Raabe (1962)
Helenium hoopesii	Helenium	-	-	-
Heuchera americana	Alumroot	Caramel	*A. mellea sensu lato*	Raabe (1962)
Hordeum vulgare	Barley	-	-	-
Kniphofia hirsuta	Red hot poker	Fire dance	-	-
Lobelia cardinalis	Cardinal flower	Queen Victoria	-	-
Nicotiana tabacum	Tobacco	White burley	-	-

Table 2. Symptoms of *Armillaria* infection observed in plants inoculated with woody inocula of *Armillaria* three months post inoculation

Plants	***A. mellea* CG440**			***A. gallica* ANA220**		
	Number with rhizomorphs in inocula and/or soil (%)	Number of plants with epiphytic rhizomorphs (%)	Number of plants with mycelial fans (%)	Number with rhizomorphs in inocula and/or soil (%)	Number of plants with epiphytic rhizomorphs (%)	Number of plants with mycelial fans (%)
Arabidopsis thaliana	1 (33)	0	0	2 (66)	0	0
Chrysanthemum maximum	2 (50)	0	1 (25)	3 (75)	1 (25)	0
Erigeron speciosus	0	0	0	0	0	0
Fragaria × ananassa	2 (50)	0	2 (50)	2 (50)	0	2 (50)
Fuchsia magellanica	0	0	1 (33)	2 (66)	2 (66)	0
Geranium [hybrid]	0	0	0	0	0	0
Helenium hoopesii	0	0	1 (25)	2 (50)	2 (50)	0
Heuchera americana	3 (75)	0	4 (100)	3 (75)	0	1 (25)
Hordeum vulgare	2 (50)	0	2 (50)	3 (75)	1 (25)	4 (100)
Kniphofia hirsuta	0	0	1 (25)	3 (75)	0	1 (25)
Lobelia cardinalis	0	0	0	3 (75)	2 (50)	0
Nicotiana tabacum	1 (25)	1 (25)	0	1 (25)	1 (25)	0

No symptoms of *Armillaria* infection were observed in plants inoculated with agar plugs of *A. mellea* and *A. gallica* or in non-inoculated control plants. n=4 with the exception of *A. thaliana* and *F. magellanica* where n=3.

Table 3. Mortality of plants inoculated with *Armillaria* and non-inoculated controls (%)

Plants	*A. mellea* inocula			*A. gallica* inocula		Non-inoculated controls
	ELDO17 agar plugs	CG440 agar plugs	CG440 wood	ANA220 agar plugs	ANA220 wood	
Arabidopsis thaliana	0	0	0	0	0	0
Chrysanthemum maximum	0	0	1 (25)[a]	0	1 (25)[a]	0
Erigeron speciosus	2 (50)	2 (50)	2 (50)	3 (75)	2 (50)	1 (25)
Fragaria × ananassa	0	0	0	0	2 (50)[a]	0
Fuchsia magellanica	0	0	0	0	0	0
Geranium [hybrid]	0	0	1 (25)	0	0	0
Helenium hoopesii	0	1 (25)	1 (25)[a]	1 (25)	1 (25)[a]	0
Heuchera americana	0	0	1 (25)[a]	0	0	0
Hordeum vulgare	0	0	0	0	0	0
Kniphofia hirsuta	0	0	1 (25)[a]	0	0	0
Lobelia cardinalis	0	0	1 (25)	0	0	0
Nicotiana tabacum	1 (25)	0	1 (25)[a]	1 (25)	2 (50)	1 (25)

[a] dead plant had mycelial fan or epiphytic rhizomorphs. n=4 with the exception of *A. thaliana* and *F. magellanica* where n=3.

Table 4. Measurement of plant growth parameters three months post inoculation

Plants	Plant growth parameter	*A. mellea* inocula			*A. gallica* inocula		Non-inoculated control
		ELDO17 agar	CG440 agar	CG440 wood	ANA220 agar	ANA220 wood	
Arabidopsis thaliana	Height (cm)	n/a	37 (36-40)	33 (26-37)	40 (38-42)	36 (34-38)	38 (37-39)
	Wet wt (g)		5.79 (5.4-6.2)	5.49 (5.0-5.9)	5.90 (5.7-6.1)	5.44 (5.3-5.7)	5.58 (5.2-5.8)
	Dry wt (g)		5.27 (4.9-5.6)	5.00 (4.6-5.3)	5.37 (5.2-5.5)	5.01 (4.8-5.3)	5.13 (4.8-5.3)
Chrysanthemum maximum	Height (cm)	19 (12-29)	14 (5-23)	16 (10-21)	24 (23-24)	18 (12-24)	16 (14-20)
	# of stems	5 (2-6)	4 (2-6)	4 (3-5)	3 (1-4)	2 (1-3)	4 (3-8)
	Wet wt (g)	53 (14.7-93.5)	33 (17.7-58.6)	42 (19.8-60.8)	43 (20.9-59.5)	23 (5.7-35.8)	72 (52.3-103.4)
			***p* = 0.040**			***p* = 0.011**	
	Dry wt (g)	16 (9.2-23.9)	12 (8.3-17.4)	16 (13.3-18.8)	14 (8.3-20.3)	10 (5.0-10.7)	21 (15.0-33.0)
			***p* = 0.033**			***p* = 0.012**	
Erigeron speciosus	Wet wt (g)	5.9 (5.0-6.9)	7.3 (5.5-10.4)	5.7 (4.8-6.3)	6.0 (4.9-7.7)	5.6 (5.0-6.6)	6.4 (5.0-8.0)
	Dry wt (g)	5.08 (4.6-5.6)	5.89 (4.9-7.2)	5.05 (4.4-5.8)	5.2 (4.3-6.0)	5.0 (4.6-6.0)	5.2 (4.6-5.7)
Fragaria × *ananassa*	Height (cm)	n/a	9 (8-10)	11 (6-15)	11 (9-13)	10 (10-11)	10 (8-11)
	# of leaves		9 (5-10)	6 (2-9)	9 (7-12)	8 (6-12)	12 (7-17)
	Wet wt (g)		41 (31.2-46.6)	33 (24.7-51.1)	47 (42.8-51.4)	34 (24.8-47.0)	51 (41.1-76.1)
	Dry wt (g)		22 (19.3-24.2)	20 (17.5-26.0)	25 (23.7-27.0)	21 (17.8-26.0)	25 (22.3-29.0)
Fuchsia magellanica	Height (cm)	n/a	15 (11-16)	13 (12-15)	15 (13-17)	14 (11-17)	10 (4-16)
	# of flowers		49 (45-54)	32 (11-49)	18 (14-26)	27 (6-51)	16 (6-22)
	Wet wt (g)		21 (11.9-29.2)	19 (15.9-24.6)	28 (24.6-32.6)	23 (20.6-26.3)	27 (26.3-28.3)
	Dry wt (g)		8 (9.3-10.2)	8 (7.9-8.9)	10 (9.4-10.5)	9 (8.4-10.0)	9 (9.1-9.7)
Geranium [hybrid]	Height (cm)	14 (7-19)	12 (9-14)	9 (5-12)	11 (9-14)	11 (7-18)	15 (12-16)
	# of leaves	9 (4-11)	9 (5-13)	5 (1-8)	10 (6-15)	6 (5-8)	9 (8-11)
	Wet wt (g)	13 (10.8-15.6)	13 (11.1-14.7)	11 (8.9-13.3)	11 (8.3-13.0)	12 (10.1-14.5)	13 (12.1-13.9)
	Dry wt (g)	8.6 (7.8-9.9)	8.6 (7.7-9.2)	7.3 (6.4-7.0)	7.5 (6.1-8.2)	7.7 (7.3-8.3)	8.6 (8.2-9.1)
Helenium hoopesii	Height (cm)	50 (43-55)	37 (30-39)	43 (32-56)	42 (38-46)	40 (31-60)	47 (40-50)
	# of flowers	11 (9-14)	7 (2-13)	11 (5-13)	7 (5-9)	8 (7-10)	12 (8-16)
	Wet wt (g)	23 (17.4-30.2)	25 (17.8-34.3)	32 (24.9-43.5)	31 (17.2-43.2)	24 (15.7-43.1)	33 (19.9-40.0)
	Dry wt (g)	13 (12.6-13.3)	13 (11.4-14.2)	14 (10.7-17.3)	14 (11.8-15.0)	13 (10.6-14.3)	15 (12.8-17.1)
Heuchera americana	Height (cm)	17 (15-19)	18 (16-19)	17 (16-18)	16 (14-18)	18 (16-20)	17 (15-18)
	# of leaves	43 (27-72)	43 (32-49)	56 (52-60)	45 (33-55)	54 (47-62)	52 (45-65)
	Wet wt (g)	41 (29.1-52.7)	43 (33.4-56.2)	37 (17.9-50.1)	43 (20.1-53.2)	49 (43.6-59.5)	52 (40.6-65.0)
	Dry wt (g)	15 (11.2-18.0)	15 (12.2-18.2)	14 (10.6-17.6)	15 (9.0-18.2)	17 (14.4-19.8)	18 (13.9-21.2)
Hordeum vulgare	Height (cm)	21 (15-35)	23 (19-26)	19 (14-28)	20 (11-27)	29 (26-32)	20 (15-32)
	Wet wt (g)	20 (11.7-37.0)	15 (11.9-19.0)	16 (11.6-18.8)	25 (12.7-53.6)	15 (12.7-19.2)	15 (14.0-15.3)
	Dry wt (g)	10 (10.0-12.2)	11 (9.3-16.2)	12 (8.8-13.9)	11 (9.4-12.4)	13 (11.0-16.6)	11 (9.9-13.6)
Kniphofia hirsuta	Height (cm)	47 (42-52)	35 (26-39)	45 (36-52)	35 (26-39)	37 (29-45)	32 (23-49)
	# of leaves	26 (20-35)	27 (15-40)	39 (29-50)	31 (11-49)	20 (12-35)	26 (14-36)
	Wet wt (g)	53 (44.2-76.9)	36 (20.6-54.8)	34 (4.7-60.0)	33 (11.8-50.0)	39 (18.2-65.1)	28 (12.8-51.3)
	Dry wt (g)	13 (11.7-15.5)	10 (6.07-15.2)	10 (4.2-15.9)	9 (5.9-11.4)	11 (7.2-12.0)	9 (5.8-13.9)
Lobelia cardinalis	Height (cm)	81 (60-100)	80 (57-96)	71 (43-91)	78 (70-88)	86 (65-103)	93 (63-125)
	# of stems	5 (3-7)	4 (2-6)	3 (2-4)	4 (3-6)	3 (2-5)	4 (2-5)
	Wet wt (g)	55 (34.6-67.8)	45 (21.5-75.6)	51 (26.3-66.7)	44 (22.3-48.0)	40 (4.8-55.8)	64 (62.3-72.6)
	Dry wt (g)	18 (14.8-20.4)	18 (15.7-20.2)	16 (12.8-17.2)	16 (14.3-17.0)	14 (4.5-17.2)	19 (18.6-21.1)
Nicotiana tabacum	Height (cm)	25 (17-36)	36 (26-45)	28 (21-32)	30 (21-42)	31 (23-40)	27 (18-30)
	# of leaves	14 (12-15)	13 (10-15)	13 (11-16)	15 (12-16)	13 (12-16)	14 (11-15)
	# of flowers	5 (3-8)	10 (6-13)	8 (6-10)	9 (0-15)	8 (1-15)	8 (0-12)
	Wet wt (g)	27 (21.8-30.3)	25 (18.3-34.5)	21 (11.4-27.3)	22 (11.2-33.1)	22 (10.2-35.2)	25 (17.2-31.9)
	Dry wt (g)	9 (8.4—9.3)	9 (8.9-10.1)	8 (8.1-8.8)	10 (8.8-10.4)	9 (8.6-10.0)	9 (5.6-9.9)

Data range is shown in brackets. The *p* values are shown in bold when the difference was significant at $p \leq 0.05$ as determined by Dunnett's post-hoc test following one-way ANOVA. n=4 with the exception of *A. thaliana* and *F. magellanica* where n=3.

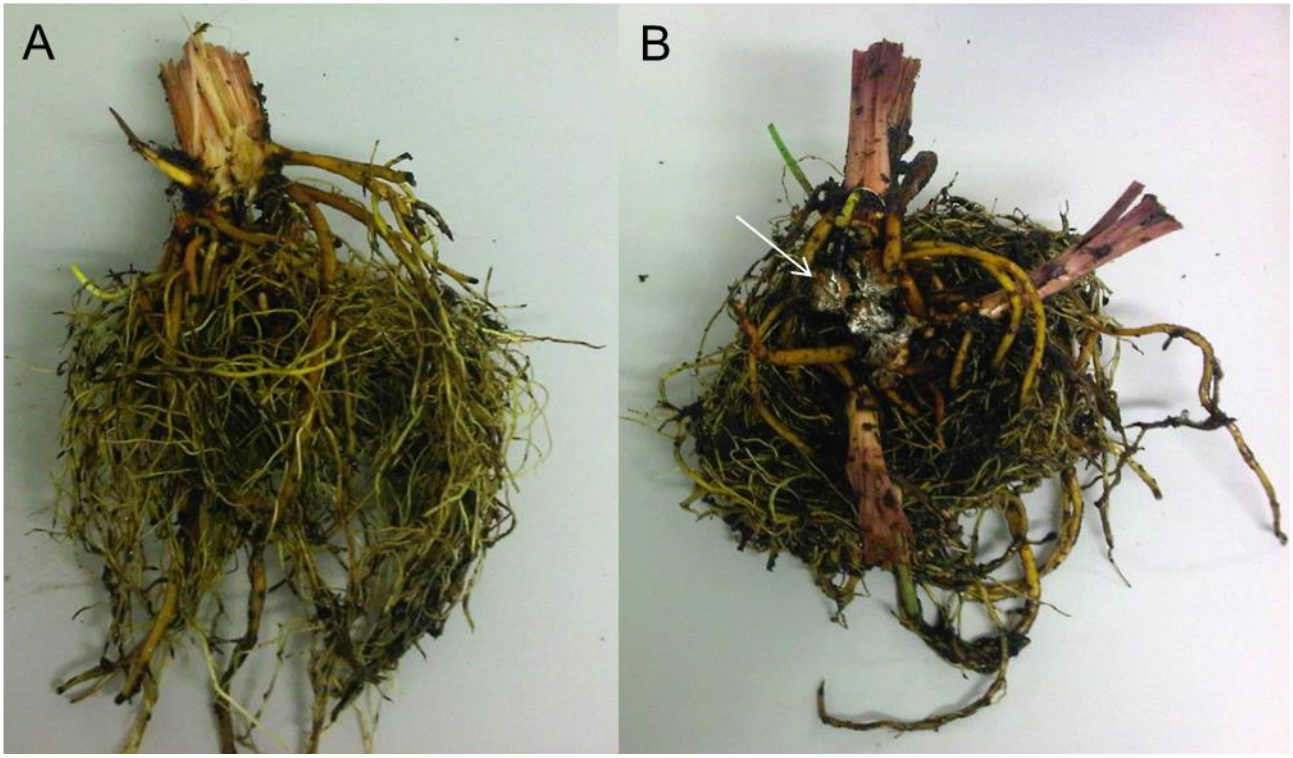

Figure 1. Root system of *Kniphofia hirsuta* harvested three months post inoculation*:* A) mock-inoculated control plant showing a healthy stem base and root system with no mycelial fans and B) *K. hirsuta* inoculated with wood inoculum of *A. mellea* CG440 showing mycelial fan in base of stem (indicated by arrow).