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Lack of effective resistance to the virulent race of *Colletotrichum lentis* in *Lens culinaris* Medikus subsp. *culinaris*

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Abstract

Anthracnose caused by *Colletotrichum lentis* is an important fungal disease of lentil in western Canada. Two known pathogenic *C. lentis* races, race 0 and race 1 have been identified and current cultivars of lentil have little or no resistance to the virulent race 0. Seven *Lens culinaris* subsp. *culinaris* landrace accessions were previously reported to have resistance to *C. lentis* race 0. In this study, accession VIR-2633, with reported resistance to both races of *C. lentis*, and seven accessions were assessed for race 0 resistance relative to LR-59-81, an interspecific line derived from a *L. culinaris* subsp. *culinaris* × *Lens ervoides* cross. The results showed a lack of effective resistance to race 0 among the tested *L. culinaris* accessions when compared to that of LR-59-81. A few sublines displayed modest improvements in resistance compared to the susceptible check 'Eston', but were significantly more susceptible than LR-59-81. Moreover, screening of the sublines of accession VIR-2633 identified 12 sublines with resistance to race 1, but all VIR-2633 sublines were susceptible to race 0. The study underlined the importance of wild lentil germplasm for broadening the genetic base of cultivated lentil and their usefulness in disease screening experiments as positive checks.

Keywords: anthracnose, disease resistance, landrace accessions, lentil, wild lentil

Introduction

Lentil (*Lens culinaris* Medik. subsp. *culinaris*), a cool season food legume cultivated around the world, is ranked fourth in global production among pulse crops (FAOSTAT, 2017). Canada accounted for 46% of the world's lentil production from 2013 to 2017 (FAOSTAT, 2017), mostly from the province of Saskatchewan (Canadian Grain Commission, 2018). Since its first report from the province of Manitoba 30 years ago (Morrall, 1988), anthracnose caused by the fungal pathogen *Colletotrichum lentis* (Damm) (Damm *et al*., 2014), has become the most important foliar fungal disease of lentil in western Canada. The disease is considered of minor importance in other parts of the world, and has been reported from Bangladesh, Bulgaria, Brazil, Ethiopia, Morocco, Pakistan, Syria and USA (Bellar and Kebabeh, 1983; Bayaa and Erskine, 1997; Morrall, 1997; Kaiser *et al*., 1998).

Two pathogenic races of *C. lentis* were previously identified (Buchwaldt *et al*., 2004) and re-designated as race 0 and race 1 (Banniza *et al*., 2018). Race 1 is a less virulent race to which partial resistance was found in a number of *L. culinaris* subsp. *culinaris* accessions (Buchwaldt *et al*., 2004, 2018). Resistance to this race was effectively transferred into elite lentil breeding lines and resulted in the release of a number of cultivars with partial resistance to race 1 in lentil production (Vandenberg *et al*., 2002, 2006; Government of Saskatchewan, 2019). However, no effective resistance was identified among *L. culinaris* subsp. *culinaris* germplasm to the highly virulent race 0 (Buchwaldt *et al*., 2004). More recently, Shaikh *et al*. (2013) evaluated 579 accessions from 20 countries of central and eastern Europe by self-pollinating plants and then making single plant selections of progenies. They reported 7, 1 and 15 *L. culinaris* subsp. *culinaris* landrace accessions with resistance to race 0, to both race 0 and race 1, and to race 1, respectively.

Wild species of lentil in the primary gene pool, *L. culinaris*, *L. orientalis* and *L. tomentosus* have little or low

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levels of resistance to race 0 (Tullu *et al.*, 2006). Among the seven lentil taxa, *Lens ervoides* (Brign.) Grande of the tertiary gene pool (Wong *et al.*, 2015) had the highest frequency of resistant accessions for both races of *C. lentis* (Tullu *et al.*, 2006). Anthracnose resistance from *L. ervoides* accessions was successfully transferred to *L. culinaris* germplasm using embryo rescue techniques (Fiala *et al.*, 2009; Tullu *et al.*, 2013) to develop two interspecific recombinant inbred line (RIL) populations (LR-59: *L. culinaris* subsp. *culinaris* 'Eston' × *L. ervoides* L01-827A; LR-26: *L. culinaris* subsp. *culinaris* 'Eston' × *L. ervoides* IG 72815). Fiala *et al.* (2009) identified the highly resistant RIL (LR-59-81) from the LR-59 population which is now used as a resistant check for disease screening for both races of *C. lentis*.

The current study was initiated to evaluate the previously reported promising sources of resistance to *C. lentis* race 0 in *L. culinaris* subsp. *culinaris* landrace accessions (Shaikh *et al.*, 2013) in relation to the resistance identified in LR-59-81. The hypothesis was that the identified *L. culinaris* subsp. *culinaris* landrace accessions possess a source of resistance to *C. lentis* race 0 that is comparable to the resistance of line LR-59-81, the interspecific resistant check for *C. lentis* race 0.

Materials and methods

Plant materials

The lentil accessions used for the current study were selected based on Shaikh *et al.* (2013). Seeds for eight *L. culinaris* subsp. *culinaris* accessions were obtained from Plant Gene Resources of Canada (PGRC), Saskatoon (Table 1). Seven were previously reported to be resistant to race 0 and accession VIR-2633 was reported to have resistance to races 0 and 1 of *C. lentis* (Shaikh *et al.*, 2013). For all eight accessions, 35 arbitrarily selected seeds, which will be referred to as 'sublines' in this paper, were planted individually in 1 gallon pots in a growth chamber. The sublines were grown to generate seeds for a replicated pathogenicity test. Seeds were harvested from each plant separately and each subline was treated as an independent entry. For each of the eight accessions, 31 sublines were used for disease evaluation in individual experiments. *L. culinaris* subsp. *culinaris* cultivars 'Eston' (susceptible to both races) and 'CDC Robin' (susceptible to race 0, partially resistant to race 1), as well as interspecific recombinant inbred line LR-59-81 derived from the cross *L. culinaris* subsp. *culinaris* cultivar Eston × *L. ervoides* L01-827A (high levels of resistance to both races) were used as checks (Fiala *et al.*, 2009; Vail *et al.*, 2012).

Thirty-one sublines of each accession, in 10 replicates were used for each experiment and the experiments were conducted separately per accession. Two seeds of each subline were sown in each cell of 38-cell cone trays (26.8 cm × 53.5 cm) filled with Sun Gro Horticulture Sunshine Mix LA4 (Sun Gro Horticulture, Bellevue, USA) and perlite (Specialty Vermiculite Canada, Winnipeg, MB) at a 3:1 ratio. Ten replicate trays per accession were arranged in a randomized complete block design and the three checks were included in each tray. The experiments were conducted under controlled conditions in a growth chamber (Conviron, Model GR178; Winnipeg, MB) and in a greenhouse at the University of Saskatchewan. The day/night temperature of 21/18 and 23/22°C, and photoperiod of 16 and 17 h were maintained throughout the experiment using artificial light sources for growth chamber and greenhouse, respectively. After germination, the developing seedlings were thinned to one seedling/cell and a soluble mixture of N, P and K (20:20:20) at 2 g/l water was applied once per week.

Fungal inoculum production, inoculation and disease assessment

C. lentis isolates CT-30 (race 0) and CT-21 (race 1) (Banniza *et al.*, 2018) were used for inoculations in separate experiments. Conidia were revitalized on 50% oatmeal agar plates (30 g oatmeal [Quick Oats, Quaker Oats Co., Chicago, IL, USA], 8.8 g agar [Difco, BD®, Sparks Glencoe, MD, USA], 1 litre H_2O) and incubated for 7–10 d at room temperature. Plates were then flooded with sterile deionized water and conidia were harvested by scraping the colonies with the edge of a sterile glass microscope slide. The suspension was collected and filtered through one layer of Mira-cloth into a clean Erlenmeyer flask. The concentration of the conidia suspension was adjusted to 5×10^4 conidia/ml using a haemocytometer. The surfactant Tween 20 (polyoxyethylene sorbitan monolaurate) was added at the rate of 1–2 drops per 1000 ml of suspension and the suspension was shaken well before inoculation.

Four weeks after seeding, plants were inoculated with the spore suspension at 3 ml per plant using an airbrush. The inoculation for one accession (VIR-2633) was conducted in a growth chamber and for seven accessions (VIR-2058, VIR-2068, VIR-2076, VIR-2080, VIR-2086, VIR-2826 and VIR-2827) in the greenhouse. For VIR-2633, sublines were inoculated with *C. lentis* CT-30 and CT-21 in separate experiments in a growth chamber. Twelve sublines of accession VIR-2633 that showed race 1 resistance after growth chamber inoculation were inoculated with both races for further confirmation in the greenhouse. Immediately after inoculation, plants were incubated at 90–100% relative humidity for 48 h in incubation chambers in the growth chamber, and for 24 h in incubation chambers in the greenhouse. They were subsequently covered

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Table 1. List of *L. culinaris* subsp. *culinaris* accessions evaluated in the current study (adapted from Shaikh *et al.* 2013)

Accession (PGRC)	Original name	Country of origin	Seed coat colour	Cotyledon colour	Resistant to race
CN 108287	VIR-2058	Czechoslovakia	Green	Yellow	Race 0
CN 108293	VIR-2068	Czechoslovakia	Green dotted	Yellow	Race 0
CN 108297	VIR-2076	Czechoslovakia	–	–	Race 0
CN 108301	VIR-2080	Hungary	Green	Yellow	Race 0
CN 108305	VIR-2086	Germany	Black	Red	Race 0
CN 108445	VIR-2826	Unknown	Green	Yellow	Race 0
CN 108446	VIR-2827	Czechoslovakia	Green	Yellow	Race 0
CN 108424	VIR-2633	Georgia	Tan	Red	Race 0 and 1

with clear plastic bags or sleeves, before being moved to regular growth chamber or greenhouse benches. In the growth chamber experiments, leaf wetness was maintained by misting water inside the bag until the final scoring. In the greenhouse, benches were equipped with 30 s misting every 90 min. Individual plants were scored for *C. lentis* disease severity at 8–10 d post-inoculation (dpi), using a 0–10 rating scale with 10% increments in anthracnose severity. Data were converted to percentage/proportion disease severity using the class midpoints for data analysis.

Data analysis

Statistical analyses were conducted using SAS software (SAS 9.4, SAS Institute, Cary, North Carolina, 2011). Disease scores of each accession (31 sublines entry in 10 replicates) were analysed separately. Normality and variance homogeneity of the residuals were tested using a Shapiro–Wilk normality test and Levene's test for homogeneity, respectively. The data did not conform to the assumptions of a Gaussian distribution. As a result, a generalized linear mixed model with a beta distribution function was fitted to the data using PROC GLIMMIX with the LOGIT link function (SAS 9.4). The genotypes were treated as a fixed factor and replicates as a random factor. Means of the disease reactions were compared for *post hoc* comparison using Tukey's honestly significant difference at $\alpha = 0.05$.

Results

Eight *L. culinaris* subsp. *culinaris* landrace accessions identified previously as promising sources of resistance to *C. lentis* (Shaikh *et al.*, 2013) were evaluated to determine their reaction to *C. lentis*, especially against the virulent race of the disease (Table 1). In greenhouse experiments, the susceptible checks 'Eston' and 'CDC Robin' had similar mean disease severity ranging from 93 to 95% in all experiments (Fig. 1). Whereas the race 0 resistant check LR-59-81 had a disease severity of 14–36%, which was significantly lower than that of susceptible checks 'Eston' and 'CDC Robin' in all experiments ($P < 0.05$). Among the 217 sublines derived from VIR-2058, VIR-2068, VIR-2076, VIR-2080, VIR-2086, VIR-2826 and VIR-2827 (31 sublines per accession), all sublines were significantly more susceptible to *C. lentis* race 0 isolate CT-30 than the resistant check LR-59-81 (Fig. 1). Disease severity for the majority of the sublines was similar to those of the susceptible checks 'Eston' and 'CDC Robin' ($P > 0.05$). The overall mean disease severity of the accessions VIR-2058, VIR-2068, VIR-2076, VIR-2080, VIR-2086, VIR-2826 and VIR-2827 ranged from 88 to 93% and no disease severity scores of less than 80% were observed for any of the sublines of those accessions (Fig. 2). Accession VIR-2826 had an overall mean disease severity of 90%, but two of its sublines had mean disease severity scores of 65 and 77%, which was significantly lower than that of the susceptible checks 'Eston' and 'CDC Robin'.

Inoculations of accession VIR-2633, previously identified as a potential source of resistance to both races of *C. lentis* race 0 isolate CT-30 in growth chamber experiments, revealed the levels of anthracnose severity ranging from 58 to 84%, with an overall mean of 72%. The susceptible checks 'Eston' and 'CDC Robin' had a mean disease severity of 94 and 88%, respectively (Fig. 3). The resistant check LR-59-81 had a mean anthracnose severity of 29%, which was significantly lower than that of all sublines of VIR-2633 ($P < 0.05$). The subline CN108424-15 had the lowest mean anthracnose severity (58%), significantly lower than that of the susceptible checks 'Eston' and 'CDC Robin' ($P < 0.05$) in the growth chamber, but under greenhouse conditions, where scores were higher overall, anthracnose severity was similar to that of the susceptible checks 'Eston' and 'CDC Robin' (data not shown).

Screening of VIR-2633 with the race 1 isolate CT-21 in the growth chamber revealed varying levels of resistance, with disease scores ranging from 5% (small lesion at stem base) to 95% (dead plant) and an overall mean of 49%. The resistant checks LR-59-81 and 'CDC Robin' had mean scores of

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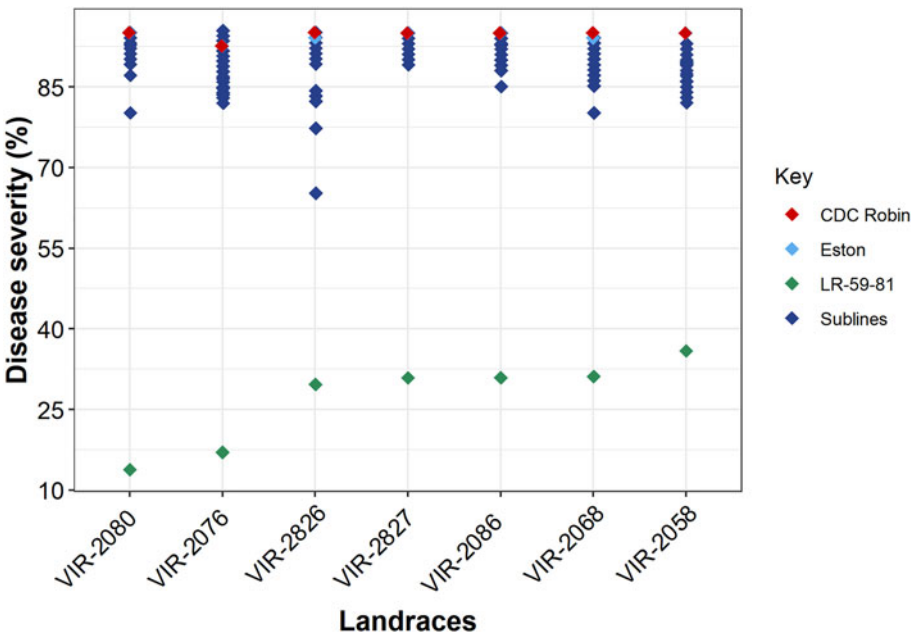

Fig. 1. Anthracnose severity for seven *L. culinaris* subsp. *culinaris* landrace accessions and checks evaluated under greenhouse conditions in response to infection with *C. lentis* isolate CT-30 (race 0). Purple data points on the panel represent mean anthracnose severity values of 31 sublines evaluated for each landrace accession in comparison with susceptible checks CDC Robin and Eston, and resistant check LR-59-81. Each data point is the estimate based on 10 replications per subline and per check. Anthracnose severity was rated using a 0–10 scale with 10% increments in disease severity.

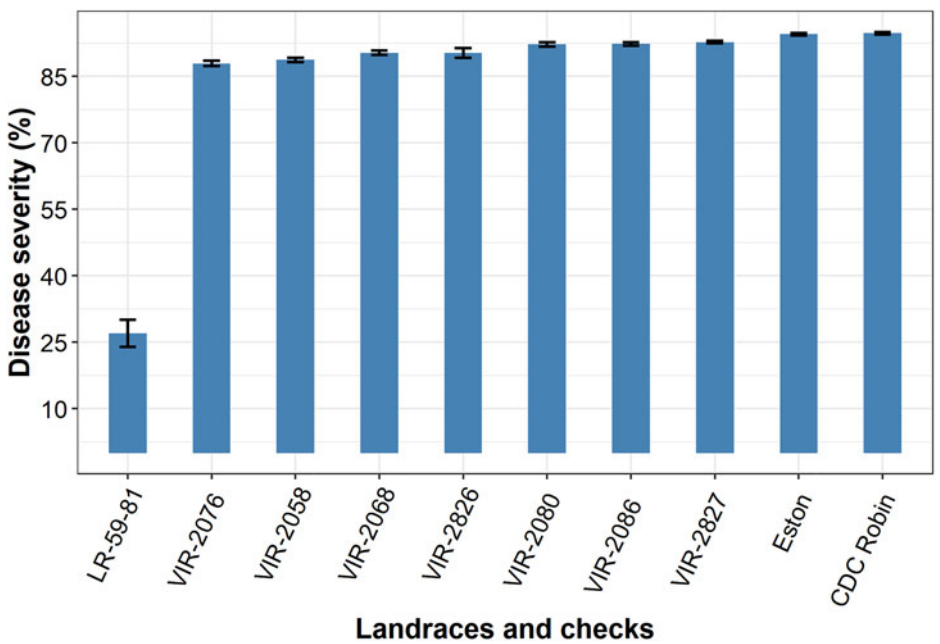

Fig. 2. Overall mean anthracnose severity score of seven *L. culinaris* subsp. *culinaris* landrace accessions and checks infected with *C. lentis* isolate CT-30 (race 0). The data are the means of 10 replications of 31 sublines evaluated for each landrace accession and for 10 replications for each, susceptible checks CDC Robin and Eston, and resistant check LR-59-81. Error bars indicate ±standard error of the mean. Anthracnose severity was rated using a 0–10 scale with 10% increments in disease severity.

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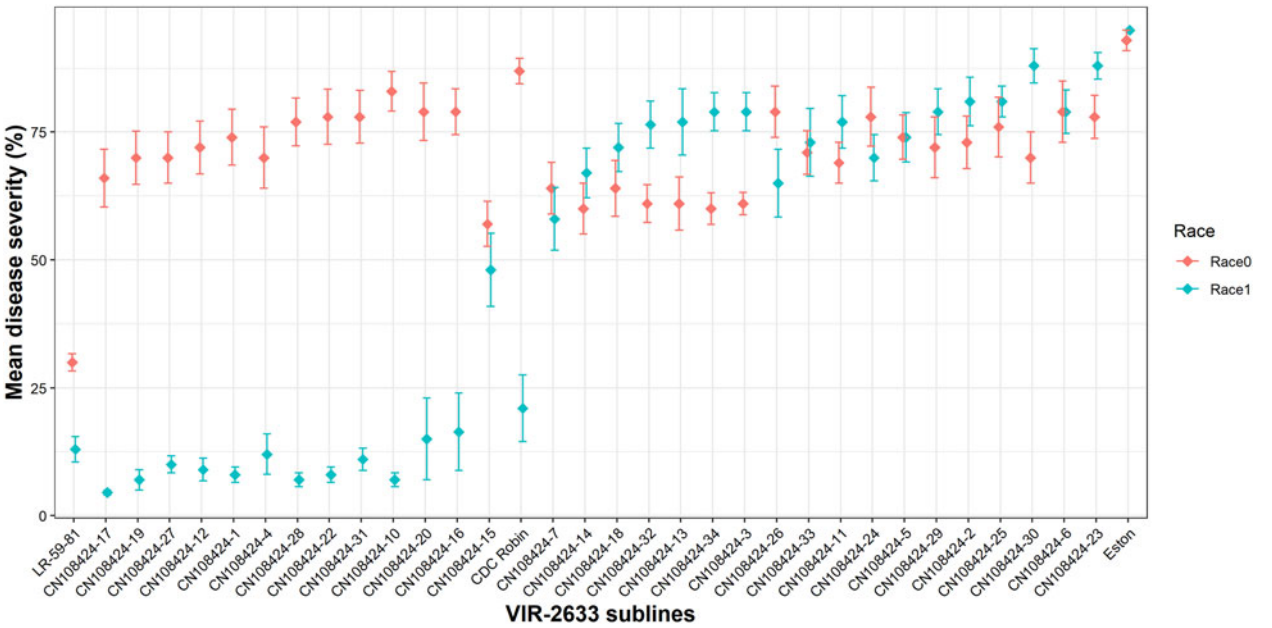

Fig. 3. Percent anthracnose severity of 31 sublines of *L. culinaris* subsp. *culinaris* landrace accession VIR-2633 evaluated under growth chamber conditions for disease reaction to race 0 and race 1. Error bars indicate ±standard error of the mean. Anthracnose severity was rated using a 0–10 scale with 10% increments in disease severity.

13 and 21%, respectively. Of the 31 VIR-2633 sublines tested, 12 had scores equal to or lower than the two resistant checks and were considered resistant. When re-tested in the greenhouse, these 12 sublines had mean disease severity scores ranging from 11 to 33%, which was not significantly different from the resistant checks LR-59-81 (28%) and 'CDC Robin' (23%), but lower compared to the 95% score for the susceptible check 'Eston' (Fig. 4). When re-tested with race 0 in the greenhouse they had a minimum average disease severity score of 72%, which was not different from the susceptible checks 'CDC Robin' and 'Eston', but was significantly higher than that of the resistant check LR-59-81 with a mean of 38%. This result indicated there was no resistance to race 0 in accession VIR-2633, but 12 sublines of the accession had scores equal to or lower than the two resistant checks and were considered resistant to race 1.

Discussion

Identification of new sources of resistance from landraces and subsequent introduction into an elite cultivated background can be efficient, and is easily implemented in breeding programmes with the goal of developing a variety with desired genes/alleles. For *C. lentis* race 0, the sources of resistance in the cultivated species and its primary genepool remain limited (Buchwaldt *et al.*, 2004; Tullu *et al.*, 2006). In the genus *Lens* the most effective resistance to both races were identified in *L. ervoides* and *L. lamottei* Czefr. (Tullu *et al.*, 2006). However, interspecific hybridization with species in genetically distant gene pools is complicated by pre- and post-fertilization barriers, such as reduced pollen fertility, chromosomal aberrations and embryo abortion (Abbo and Ladizinsky, 1991, 1994; Gupta and Sharma, 2007). Fiala *et al.* (2009) and Tullu *et al.* (2013) used ovule and embryo rescue techniques to transfer the resistance from the *L. ervoides* accessions into *L. culinaris* subsp. *culinaris* germplasm. The resultant interspecific hybrid RIL lines had variable levels of fertility in subsequent segregating populations.

The interspecific RIL LR-59-81 (Fiala *et al.*, 2009) has become a commonly used resistant check in all anthracnose disease screening nurseries and indoor assays at the Crop Development Centre (CDC), University of Saskatchewan. This RIL has shown consistently higher levels of resistance to both races in greenhouse and field evaluations, even under high disease pressure (Fiala *et al.*, 2009; Vail, 2010), and the resistance is not dependent on plant age (Vail, 2010). Moreover, the response of LR-59-81 to the inoculation of 144 ascospore-derived *C. lentis* populations (race 0 × race 1) revealed lower levels of stem lesions and shoot die-back to all isolates of that population (Banniza *et al.*, 2018).

Evaluations of anthracnose severity under controlled conditions in the current study confirmed the lack of high levels of resistance to race 0 in *L. culinaris* subsp. *culinaris* accessions in comparison with the resistance level of LR-59-81. We found a few sublines that had improved resistance when compared to the susceptible check 'Eston'.

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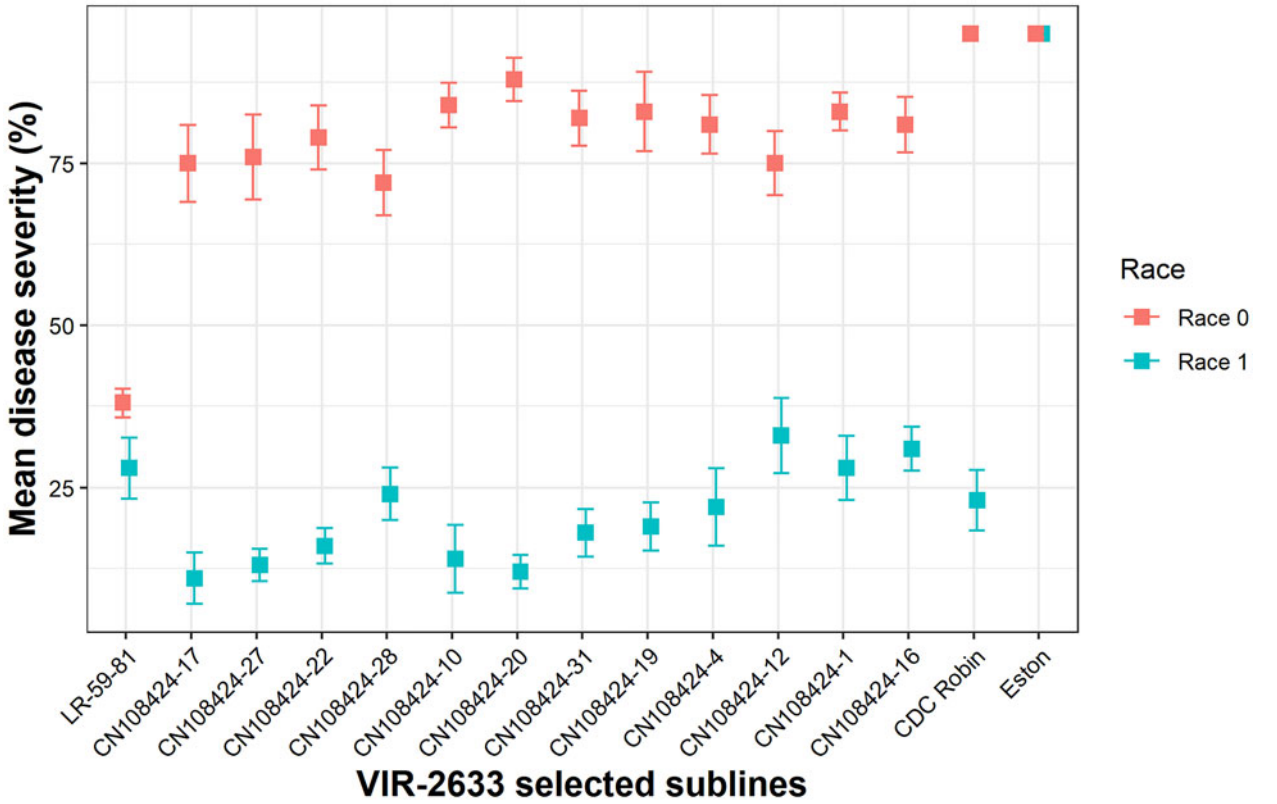

Fig. 4. Percent anthracnose severity of 12 sublines of *L. culinaris* subsp. *culinaris* landrace accession VIR-2633 resistant to race 1 evaluated under greenhouse conditions for both race 0 and race 1 reactions for further confirmation. The 12 sublines were selected after growth chamber inoculation for race 1. Error bars indicate ±standard error of the mean. Disease was rated using a 0–10 scale with 10% incremental increases in disease severity.

This partially agrees with the findings of Shaikh *et al.* (2013). They reported that, after a cycle of selfing and single plant selection, all the lentil accessions evaluated in the study had resistance to race 0 in comparison with the susceptible check 'Eston'. However, the level of resistance in those accessions was significantly lower compared to the level of resistance of the interspecific RIL LR-59-81. A possible explanation for the discrepancy could be that landrace accessions are heterogeneous either due to segregation at resistance loci or are a mixture of different genotypes. The success of finding the desired level of resistance in such situations mainly relies on the frequency of targeted alleles in the accession. In VIR-2633, identified as a potential source of resistance to both races, 38.7% of the tested sublines were resistant to race 1, while none of them showed resistance to race 0. Another possible reason could be differences in race 0 isolates used for the two studies. It is possible that the race 0 isolate used in the current study was more virulent, potentially indicating a higher aggressiveness on *L. culinaris* subsp. *culinaris* accessions in comparison with the resistant check. Similar results were reported by Vail (2010), who evaluated the resistance to both races for accession VIR-421 under field conditions, which had previously been reported to be resistant to race 0 (Buchwaldt and Diederichsen, 2004). Banniza *et al.* (2018) also found only modest improvement in resistance of VIR-421 compared to 'Eston', and that it significantly lower resistance compared to LR-59-81 when tested against an ascospore-derived population of *C. lentis* from a cross of CT-30 (race 0) × CT-21 (race 1).

Based on these results, it was confirmed that sources of high levels of resistance to race 0 of *C. lentis* appear to be restricted to wild *Lens* species, especially accessions of *L. ervoides* as reported by Tullu *et al.* (2006). Exploiting the resistance in the tertiary gene pool species can be confounded by linkage drag (Tanksley and Nelson, 1996). The use of marker-assisted selection (Collard and Mackill, 2008) may improve resistance breeding strategies for transferring race 0 resistance genes from *L. ervoides* without the associated linkage drag. This may require deeper knowledge of genomic information considering that *L. culinaris* and *L. ervoides* have a chromosomal translocation between chromosomes 1 and 5 (Gujaria-Verma *et al.*, 2014; Bhadauria *et al.*, 2017). The transfer of the desired genes/alleles between the two species is possible only if the genes/alleles that control the resistance are not near the

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translocation breakpoint. The identification of quantitative trait loci in the intraspecific *L. ervoides* population LR-66 (Bhadauria *et al.*, 2017) is the first step towards identifying resistance loci relative to that breakpoint.

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