



Fig. 7. Conceptual model of spread of a) necrotic and b) non-necrotic BYMV dispersing from a point source focus (single infected plant) to regions defined by three concentric rings: A (inner), B (middle) and C (outer), at five different points over time. Depth of shading indicates proportion of lupin plants newly infected during previous time period according to proposed infection curves shown in graph on lower right. Legend for graphs: A— solid line — B- - - - - C— ····· cumulative infections within A— thick solid line .

over time in this situation is sigmoidal, denoting a polycyclic type of spread, as expected with non-necrotic BYMV. This is in contrast to the near monocyclic nature of spread for necrotic BYMV in lupins in the absence of internal clover infection foci (Jones, 1993, 1994b; Cheng *et al.*, 2002).

Our conceptual models illustrate how spatial spread patterns between the two BYMV types differ. This was clearest at the 'natural spread site' where clustering indices for the non-necrotic type were larger and increased over time while those for the necrotic type were smaller and remained constant. However, here, the overall proportion of plants infected with non-necrotic BYMV was small. Throughout most of the lupin block, region A (Fig. 7b) around the initial infected plants did not reach its maximum infection rate and there was no decline in overall clustering at the end of the growing season. In contrast, in Expt 3 spread of non-necrotic BYMV around initial introduced infection foci approached its maximum rate. A drop off in infection over time in the central area of such plots was evident (Fig. 6), in agreement with its conceptual model. Over time, there was a decline in the contrast between infection patch and gap throughout the plots and a decrease in the clustering indices, which was clearest in the plot with introduced non-necrotic foci removed late. Because introduced necrotic clover infection foci did not die and were present for part of the growing season, as expected the pattern of spread of necrotic infection in Expt 3 deviated from the conceptual model for this type, moving over time towards the conceptual model for the non-necrotic type. Away from the perimeter of lupin crops, plants with necrotic symptoms are usually found isolated or in pairs. However, occasionally with wide row spacing limited, staggered infection spreading along rows on either side of an initial infected plant is sometimes evident. This staggered spread illustrates the different phased cycles of infection with necrotic BYMV implied in the conceptual model.

Strong spatial association between assessment dates was attributable mostly to association between BYMV infection gaps rather than patches. However, at the 'natural spread site', positive associations between patches of infection were considerably more numerous for the non-necrotic than the necrotic type, especially later in the growing season when the epidemic was larger. This confirmed the less diffuse nature of spread of non-necrotic BYMV. The locations of earlier BYMV infections had a greater influence on occurrence of new infections with non-necrotic than necrotic BYMV. With the latter, new infections relied mainly upon new arrivals of viruliferous aphid vectors from external necrotic BYMV sources. In the experiments, within plots with introduced clover infection foci of homologous type there were no clear differences in spatial

association over time between the two introduced BYMV types, presumably due to the presence of the introduced clover foci throughout (Expt 2) or initially (Expt 3). Within plots without introduced foci or with introduced foci of opposite type, association was weaker than in plots with introduced foci of homologous type and there were no clear differences in association between the two types, due to relatively few new infections at each assessment. In all plots in the experiments and at the 'natural spread site', for both BYMV types, the strongest associations were between assessment dates 1-3 wk apart, corresponding with the approximate delay between initial infection and first appearance of obvious systemic symptoms. Although remaining positive, association declined as the season progressed and was seldom statistically significant with dates more than 5 wk apart. The conceptual models help to explain this as at first, with only a small amount of infection, there is a large degree of association both between infection gaps and between infection patches. As the initial infection areas become saturated the proportion of new infections declines and association between dates becomes weaker, although the larger outer regions where infection rates remain relatively small still ensure it remains positive overall. Towards the end of the growing season, association is further weakened due to few new infections occurring anywhere because there are not many uninfected plants left and/or aphid vectors are absent.

The comprehensive nature of spread of non-necrotic BYMV has implications for lupin grain yield losses, since there is less potential for compensatory growth by nearby healthy plants, than where increased growth of healthy plants can fill in gaps left when isolated necrotic plants die (Jones, 1993). In addition, the faster spread of non-necrotic BYMV (Cheng *et al.*, 2002) results in substantially greater virus incidence, in turn causing larger overall yield losses despite the more severe impact of necrotic BYMV on yield of individual infected lupin plants (Cheng & Jones, 1999b; Jones *et al.*, 2000; Jones & Coutts, 2002). As with the study of temporal BYMV spread in lupin (Cheng *et al.*, 2002), this spatial investigation therefore clearly demonstrates how systemic hypersensitive (necrotic) virus resistance can be deployed to diminish virus spread and resulting yield losses in the field. However, it also shows the limitations associated with deploying virus resistance that is strain specific, since the yield benefits are lost when infection fails to induce a hypersensitive response.

SADIE provided a rigorous and quantitative means for assessing the difference in size and significance of infection clusters between the two BYMV types. In most situations, within individual plots, one type of BYMV spread more quickly than the other. This

made it important to employ a method like SADIE that describes the spatial features of a set of counts independent of their numeric properties. The SADIE approach to the study of spatio-temporal dynamics differs from traditional techniques that use an individual time series as the unit. It focuses on the spatial structure and establishes the temporal component by evaluating the evolution of this structure over time. This is achieved by quantifying the similarity between two patterns from different occasions, through the degree of spatial association between them (Winder *et al.*, 2001; Perry & Dixon, 2002). SADIE was used previously to quantify spatio-temporal relationships within virus spread data (Korie *et al.*, 2000). Our study confirms it to be a valuable tool with widespread application in the analysis of spatial patterns of virus spread.

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