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Author(s): Dan L. Johnson, Jon Lovett Doust and G. W. Eaton
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THE EFFECT OF EUROPEAN CANKER AND ITS SPATIAL PATTERN ON FOUR APPLE CULTIVARS IN BRITISH COLUMBIA

By DAN L. JOHNSON, JON LOVETT DOUST* AND G. W. EATON

Department of Plant Science, University of British Columbia, Vancouver, British Columbia, Canada V6T 2A2

SUMMARY

(1) The density and distribution of European canker (*Nectria galligena*) on all combinations of four scion and interstock cultivars in an orchard of 10 yr old trees in the Lower Mainland of British Columbia were determined.

(2) There was no effect of interstock cultivar upon tree mortality, but there were large scion cultivar effects. The numbers of cankers and degree of aggregation of cankers on surviving trees followed a pattern similar to that of tree mortality. Trees of the cultivars 'Summerland Red McIntosh' and 'Harrold's Delicious' were quite susceptible to buildup of canker and subsequent death, while 'Spartan' and 'Golden Delicious' proved relatively resistant.

(3) Multiple regression analysis indicated that the number of cankers per tree was significantly related to the sum of the cankers on the eight surrounding neighbours of each tree.

(4) Trunk cross-sectional area was significantly correlated with the number of cankers per tree on McIntosh and Spartan trees. However, it was shown that differences in tree size alone did not account for the differences in numbers of cankers on the four scion cultivars.

(5) It was concluded generally that scion cultivar and European canker may act in conjunction and result in a heterogeneously stunted apple orchard.

INTRODUCTION

European canker, *Nectria galligena* Bres., is a common fungal parasite of apple and other hardwood trees. Infection of apple trees is known to be influenced by several biological and meteorological factors, including moisture regime, conidium concentration (Dubin & English 1974), spore source, season (Dubin & English 1975) and differential varietal resistance (Zagaja *et al.* 1971; Borecki, Czynczyk & Millikan 1978). Dublin & English (1975) showed further that (asexually produced) conidia were the major infective propagules, while (sexually produced) ascospores played only a negligible role in infection. They determined that disease development was influenced by leaf fall, temperature and rainfall effects.

Characteristically, infected trees show death of localized areas of bark and underlying cambium on the trunk and branches. Trees slough off dead bark from the face of the canker, frequently leaving a blackened, ellipsoid series of concentric callus ridges.

As part of an ongoing study (see also Eaton & Meehan 1972; Eaton & Robinson 1977; Jentsch 1981), a 10-yr-old experimental orchard comprising four commercial apple cultivars in all combinations of scion and interstock has been examined, to study the

* Present address: Department of Biology, Amherst College, Amherst, Massachusetts 01002, U.S.A.

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influence of cankers on tree growth and mortality. In addition characteristics of the distribution of *Nectria* cankers were considered, within the orchard and on single trees. It was generally considered that this orchard consisted of stunted trees that lacked the growth and vigour normally associated with trees of similar age in commercial orchards.

We were interested in the following questions concerning European canker: Had tree death occurred differentially, according to either scion cultivar or interstock cultivar? Were cultivars distinguished by the numbers of cankers which they bore? Was any spatial pattern of canker density apparent in the orchard? What effect did scion and cankers have upon tree growth as measured by increments in trunk girth?

METHODS

Four apple cultivars: 'Summerland Red McIntosh', 'Spartan', 'Harrold's Delicious' and 'Golden Delicious' were established in all sixteen possible combinations of scion and interstock, all on Malling 9 rootstock and planted in 1971 at the University of British Columbia experimental orchard. The experimental design consisted of four complete blocks with forty-eight trees (four of each combination) arranged completely at random within each block. The 256 trees were spaced at 2 m × 4 m.

Periodically from 1971 to 1980, trees were examined for the presence of *Nectria* cankers, and infected branches were pruned. Dead or very severely infected trees were removed completely. Several fungicide applications were made each year for control of apple scab in the orchard. Nominal nitrogen fertilizer applications had been applied annually. No fungicide was applied to control European canker.

Trunk diameters were determined for each tree, using vernier calipers at a trunk height of 50 cm. Records were taken in April 1979, and again in February 1981. The increment in cross sectional area was calculated for each trunk.

In February 1981, trees were carefully examined and the frequency of *Nectria* cankers was recorded. Cankers were noted as occurring either on branches or main stems of trees.

RESULTS AND DISCUSSION

Tree mortality

By the end of the experiment in 1981 there remained: fifty-seven Golden Delicious, thirty-seven McIntosh, thirty-seven Delicious and fifty-one Spartan (see Table 1). Based on annual inspections over 10 yr by one of us (G.W.E.), all of the deaths and/or removals were attributed to damage by European canker. Scion cultivar was a highly significant factor affecting tree mortality ($P < 0{\cdot}0001$), whereas interstock cultivar was not ($P \cong 0{\cdot}6$). Previously, interstock has been found to have very little effect on leaf and fruit mineral content in these apple cultivars (Eaton & Robinson 1977).

TABLE 1. Survival of apple trees to the tenth year according to scion and interstock cultivar. Each scion-interstock combination started with sixteen trees

	Interstock cultivar				
Scion cultivar	Golden Delicious	McIntosh	Delicious	Spartan	Total (%)
Golden Delicious	16	14	14	13	57 (89·0)
Spartan	12	12	12	15	51 (79·6)
McIntosh	11	11	8	7	37 (57·8)
Delicious	10	8	9	10	37 (57·8)
Total (%)	49 (76·6)	45 (70·3)	43 (67·2)	45 (70·3)	$n = 182$

TABLE 2. Analyses of variance of canker densities. (Mean numbers for scion cultivars are shown in Table 4)

Source	df	Mean squares Main stem cankers	Branch cankers	Total cankers
Blocks	3	10·8 NS	131·0*	210·4**
Scion cultivar	3	35·8***	175·7**	356·0***
Interstock cultivar	3	1·5 NS	16·9 NS	17·0 NS
Scion × Interstock	9	3·9	33·7 NS	55·0 NS
Residual	144	5·6	35·6	52·2
Total	162			

*** $P < 0{\cdot}001$, ** $0{\cdot}001 < P < 0{\cdot}01$, * $0{\cdot}01 < P < 0{\cdot}05$.

Canker density

The number of cankers on surviving trees followed a varietal pattern which was similar to that of mortality (Table 2).

The density of cankers (i.e. number of cankers per tree) found on main stems and branches were related: trees with greater numbers of branch cankers had greater numbers on the main stem ($r = 0{\cdot}48$; $P < 0{\cdot}0001$). Branches tended on average to have more than three times as many cankers as did main stems. As with tree mortality, Delicious showed the highest canker density, closely followed by McIntosh. Golden Delicious and Spartan consistently showed a high degree of resistance.

In California, Nicols & Wilson (1956) and Dubin & English (1975) found that Delicious was the cultivar most susceptible to innoculation of *Nectria* spores. Golden Delicious was much more resistant. Dubin & English (1974) reported that cankers on the scaffold branches of Golden Delicious tended to callus over, whereas infected Delicious branches were nearly always killed.

The extreme susceptibility of Delicious and McIntosh cultivars has been reported by Zagaja *et al.* (1971) for trees grown in north-western Poland. Golden Delicious has been found to show moderate resistance in Poland to *Nectria* canker, and also to cankers caused by *Stereum purpureum* and *Pezicula* spp. (Borecki, Czynczyk & Millikan 1978). These workers also found that of their ten Spartan trees, nine exhibited large cankers and suffered occasional stem girdling, while only a single tree remained uninfected. The Spartan trees in the present experiment were resistant to the extent that there was 80% survivorship over a period of 10 yr (Table 1). There were also fewest cankers on branches of Spartan trees, compared to the other three cultivars in the experiment (Table 4).

Canker distribution

The distribution of cankers on the apple trees was of a contagious, or 'over-dispersed', nature. This is consistent with the findings of Byrde *et al.* (1973). Frequencies of canker gave good fits to the negative binomial distribution in all cases ($P > 0{\cdot}05$). In no case was the distribution of cankers on the trees random (that is, following a Poisson distribution). Variance-mean ratios were significantly greater than 1 in all cases ($z > 5$; $P < 0{\cdot}0001$). Statistics for the fitted distributions are shown in Table 3. The k-values, or 'clumping parameters', exhibit the same pattern as did mortality and canker density shown in Tables 1 and 2 (but see discussion below). The k of the negative binomial gives an indication of the degree of aggregation (Southwood 1966; Elliott 1977; Pollard 1979). A low value suggests extreme aggregation, whereas a larger k implies a more random distribution. When $k = 1$ a geometric distribution is described. In the data presented here, the more susceptible Delicious and McIntosh cultivars showed a very low to moderate degree of aggregation,

TABLE 3. Distribution statistics for canker densities. Statistics for cankers on main stems and cankers on branches are shown separately. The first two columns are the means and variances of the number of cankers per tree for four cultivars. Block differences were ignored since they were not substantial for either main stems or branches (1·1% and 6·1% of total variation respectively). The *k*-values were estimated from fits to the negative binomial distribution. Low *k*-values indicate a higher degree of aggregation than do high *k*-values

	Canker density							
	Main stem				Branches			
Scion cultivar	$\bar{x}$	s^2	stand Morisita	k	$\bar{x}$	s^2	stand Morisita	k
Golden Delicious	1·10	2·52	0·508	0·63	5·50	32·8	0·509	0·80
Spartan	1·71	5·39	0·511	0·64	5·20	38·1	0·513	1·04
McIntosh	2·36	6·43	0·508	1·10	8·36	46·1	0·507	2·25
Delicious	3·28	9·06	0·505	1·85	9·39	34·8	0·503	3·68

whereas the two relatively resistant cultivars tended to have either very few or very many cankers on a tree.

Some authors have expressed reservations about using the negative binomial as a model of dispersion. Myers (1978) found that estimates of k were correlated to sample mean. It is difficult to correct for this relationship since k is not related to $\bar{x}$ by any simple function (Taylor, Woiwood & Perry 1979). Ecological problems associated with the model have been discussed by Pielou (1977) and Taylor, Woiwood & Perry (1979). Because establishment and mortality of European canker are thought to be density-independent, and since cankers do not move once established, there are no inherent ecological reasons to preclude use of k of the negative binomial in the present study as an indicator of dispersion. Included in Table 3 is the standardized Morisita's coefficient, a dispersion index that has been shown to be independent of sample mean (Smith-Gill 1975; Myers 1978). Values greater than 0·5 indicate clumping significant at $P < 0{\cdot}01$ (Smith-Gill 1975). The trend in the standardized Morisita values agrees with that of the *k*-values. Cankers of Golden Delicious and Spartan trees exhibit more clumped distributions than do those of McIntosh and Delicious.

When data such as these exhibit contagion, an inverse hyperbolic sine transformation may be useful in normalizing residuals and adjusting variances in a least squares analysis. This procedure has been applied to *Nectria* canker data by Byrde, Clarke & Welford 1973. However, in the present case the analysis remained nearly unchanged. The transformation removed a small block effect on number of cankers per tree and slightly enhanced the already strong differences among the scion cultivars. It appears that the differences in the four blocks in the orchard may have been due to the location of a few heavily infected trees.

Spatial pattern

Since European canker can be spread between trees by aerial dispersal of conidia, it was conjectured that the number of cankers per tree would be related to the number on surrounding trees. If so, the size and cultivar of neighbouring trees would be important factors influencing the health, longevity and productivity of apple trees.

To test for a neighbour effect, the orchard was considered as a rectangular lattice (somewhat similar to the approaches described by Bartlett 1975; Pearce 1976; and Pearce & Moore 1976) in which each living tree is surrounded by eight others, each with some total number of cankers. (Dead, i.e. missing, trees had zero cankers.) In cases where a tree

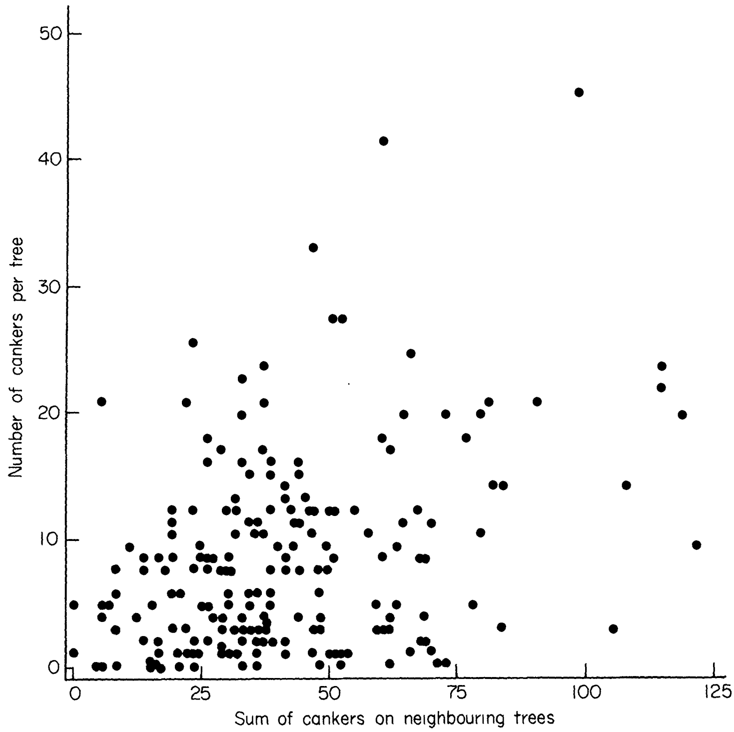

FIG. 1. The relationship between the number of cankers found on a tree and the sum of cankers on its eight immediate neighbours. Each point in the scattergram represents a single live tree.

had died, and a new tree planted in its place, the observation on the new tree was included, since it could have influenced and been influenced by its neighbours. Trees on the edge of the orchard were considered to have an outer row of neighbours with no cankers. In this way the 'edge effect' was included in the analysis.

The total number of cankers per tree was significantly correlated with the sum of the total cankers on the eight neighbouring trees ($r = 0{\cdot}333$; $P < 0{\cdot}0001$); see Fig. 1. Since it had already been shown that significant differences in canker load exist among the four cultivars in the orchard, multiple regression equation was fitted to predict the number of cankers on a tree from its scion cultivar, and from the sum of the cankers on its eight neighbours. The use of indicator variables (Neter & Wasserman 1974) allowed the inclusion of scion cultivar in the regression equation. The significant effect of neighbours was not diminished; rather it was enhanced by removal of the influence of scion cultivar (F [1,187] = 27·1). The regression equation that included scion cultivar and the sum of cankers on nearest neighbours as independent variables, explained 23·2% of the variance of total cankers per tree.

Tree size

The number of cankers per tree was weakly correlated ($P < 0{\cdot}05$) with tree size for two of the four cultivars (McIntosh and Spartan). It may be argued that part of the scion cultivar effect on canker density may have been due to size differences among the cultivars. It is felt, for the following reasons, that size is not the only determinant. The patterns of trunk size and canker density differences among the four cultivars were not

TABLE 4. Mean differences in size and canker densities for four apple cultivars. Small letters indicate similar means within a column (S.N.K. test; $P < 0.05$)

Scion cultivar	Cross-sectional area (cm^2) Mean (S.E.M.)	Total cankers per tree: Branches Mean (S.E.M.)	Total cankers per tree: Main stem Mean (S.E.M.)
Golden Delicious	17·98 a (0·82)	5·50 a (0·83)	1·10 a (0·23)
Spartan	10·35 c (0·60)	5·20 a (0·92)	1·71 ab (0·35)
McIntosh	16·13 ab (1·08)	8·36 b (1·18)	2·36 b (0·44)
Delicious	14·96 b (1·12)	9·39 b (0·98)	3·28 b (0·50)
Differences among cultivars	$P < 0.0001$	$P < 0.004$	$P < 0.0004$

TABLE 5. The mean increments in trunk cross-sectional area between July 1979 and February 1981 (cm^2). The small letters indicate means which did not differ significantly (tested by S.N.K.; $P < 0.05$).

	Golden Delicious	McIntosh	Delicious	Spartan
n	48	34	36	45
$\bar{x}$	7·46 a	4·94 b	4·29 bc	3·15 c
S.E.M.	0·53	0·82	0·57	0·33

Overall F-test of differences among means: $F(3, 159) = 12.21$ $P < 0.0001$.

consistent (Table 4). When canker density was predicted from scion cultivar and trunk size (using regression with indicator variables), absolute size proved to be a highly significant term, after the removal of the cultivar effect ($P < 0.001$).

The four scion cultivars differed in growth of stem cross-sectional area ($P < 0.0001$). Table 5 shows the mean increments in growth for the four cultivars. These follow a pattern similar to trunk size. Girdling of branches or the main stem could seriously impede continuity of the vascular cambium. There may be large growth effects and possible secondary effects upon flowering, seed set and fruit production.

This experimental orchard contained stunted trees. There was, however, variation in the degree of individual stunting. Some of this variation may be due to the uneven pruning practice and experimental nature of the orchard; yet some would also seem to be the result of the differential susceptibility of cultivars to *Nectria* canker. Larger trees generally had more cankers than smaller trees. This may be related to their greater available surface area. However, it has been shown that size alone does not account for the highly significant scion effect. A greater load of cankers can lead to a greater likelihood of tree death. McIntosh trees were biggest, had most cankers and the lowest survivorship. At the same time, Spartan trees were smallest and had fewest cankers and high survivorship. The greater mortality rate of the larger, McIntosh trees, may leave the average size of survivors in the orchard small, and the orchard tending generally towards a stunted condition.

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