Epidemiological Modeling of *Phytophthora ramorum*: Network Properties of Susceptible Plant Genera Movements in the Nursery Sector of England and Wales[1]

Marco Pautasso,[2] Tom Harwood,[3] Mike Shaw,[3] Xiangming Xu,[4] and Mike Jeger[2]

Abstract

Since the first finding of *Phytophthora ramorum* in the U.K. (on *Viburnum tinus*, 2002), the pathogen has been reported throughout the country on a variety of susceptible species both in the horticultural sector and in woodlands and historic gardens. The nursery network may have properties which affect the epidemic threshold for spread of the pathogen. Here, as part of ongoing modeling studies, we provide an analysis of the database of positive *P. ramorum* records in England and Wales (2003 to 2005), both in terms of affected plant genus and country of origin. The majority of positive findings are reported on *Rhododendron* (68 percent), with a substantial minority on *Viburnum*, *Camellia*, and *Pieris*. Another 15 genera make up the remaining 3 percent of positive records. These findings highlight the wide range of plant species at risk from the pathogen, and suggest that *Rhododendron* could act as a super-connected susceptible genus. This property would be characteristic of a scale-free network. As for the country of origin, the majority of findings originate from the U.K., but a non-negligible number (~ 30 percent) of positive records originate from several other countries. Models of network movements of plants susceptible to *P. ramorum* therefore need to take into account that this is a largely open system, with both links in and out of a single country. The number of *P. ramorum* susceptible plant species and the number of countries involved in their trade have certainly facilitated spread and pose a formidable challenge to the current effort to eradicate or contain the pathogen.

Key words: Horticultural trade, landscape pathology, networks epidemiology.

'*Phytophthora*' is Greek for plant destroyer, whilst '*ramorum*' is Latin for branched, referring to the pathogenicity of *P. ramorum* to twigs and branches of *Rhododendron* and other shrub species (Werres and others 2001). As such, *P. ramorum* would be relevant to studies in network epidemiology if only because of its name. However, this pathogen has been reported from plant nurseries in several countries (for example, Werres and others 2001; Appiah and others 2004; Parke and others 2004;

---

[1] A version of this paper was presented at the Sudden Oak Death Third Science Symposium, March 5–9, 2007, Santa Rosa, CA, USA.

[2] Division of Biology, Imperial College London, Wye Campus, TN25 5AH, Kent, U.K. For correspondence: m.pautasso@ic.ac.uk.

[3] The University of Reading, School of Biological Sciences, Lyle Tower, Whiteknights, Reading, RG6 6AS, U.K.

[4] East Malling Research, New Road, East Malling, ME19 6BJ, Kent, U.K.

Stokstad 2004; Herrero and others 2006; Tubajika and others 2006) and these nurseries form a complex directed trade network by exchanging plant material.

Networks are becoming increasingly relevant to epidemiology (for example May 2006). This is because networks such as that in global aviation can efficiently spread human diseases across the world (for example Hufnagel and others 2004). This happens for a number of reasons (for example Guimerá and others 2005): (i) the global aviation network is a giant component, which means that it is possible to fly from any airport in the world, even if not directly, to any other airport; (ii) in many cases, this is possible with a relatively low number of flights, due to the presence of international hubs, or super-connected airports; (iii) moreover, there is a high heterogeneity in the areas covered by the network, and in the strength of the links.

Networks are relevant not only to epidemiology (for example, Newman 2003). In fact, there has been an upsurge of studies applying the tools of network theory to a number of disciplines, from food web ecology to sociology and computer science (for example, Amaral and others 2000). If we attempt to bring some order to this burgeoning material according to the degree to which the analyzed networks are natural, social or technological, it is clear that epidemics have each of these characteristics: disease spread is a natural phenomenon, it is facilitated by technology (although technology also helps in preventing disease spread), and, since people are involved, epidemics are also a social issue.

Networks are sets of elements connected by links. In the context of the networks underlying the spread of *P. ramorum*, nodes can be the nurseries trading susceptible species, and links can be shipments of these plants between nurseries. Nodes can be connected in various ways, and this leads to a typology of networks (for example, Dybiec and others 2005, Keeling and Eames 2005). Local networks are modeled as more or less regular lattices. Their feature is neighboring connectivity. If we retain this neighboring connectivity but add the rewiring of some local links into shortcuts, or long-distance connections, we obtain small-world networks. If nodes are connected to other nodes randomly, in other words with a certain probability p, then the network is random. Scale-free networks are characterized by the presence of hubs, or super-connected individuals.

It turns out that, other things being equal, the structure of networks can have a profound effect on epidemic development. Simple models of disease spread in networks with constant number of nodes and links and with epidemic starting from a single infection show that the disease steady-state is first reached in scale-free networks, then in random ones, and only later in small-world and local networks (Shirley and Rushton 2005). For nurseries trading plants susceptible to *P. ramorum* or other pathogens, a SIS (Susceptible-Infected-Susceptible) model may be more realistic than the more conventional SIR (Susceptible-Infected-Removed) model (for example, Gilligan and others 1997, Jeger and others 2007). Even if lessons are learnt from past errors and best management practices are adopted, nurseries where the pathogen has been detected are still at risk of becoming infected after the pathogen has been eradicated if they continue to handle plant species susceptible to *P. ramorum*.

Measures aiming at containing the spread of *P. ramorum* in nurseries are being taken in the U.K., and there is evidence that this containment policy is effective. Figure 1 shows the temporal development of the number of positive records to *P. ramorum* in nurseries and garden centers of England and Wales (2003 to 2005; data kindly provided by the Department for Environment, Food, and Rural Affairs, U.K.; the database has on the whole 2,788 positive records to *P. ramorum* out of 81,036 tested records). As a site can have more than one positive record (because *P. ramorum* may have been found on different species and on different dates), this graph is not the same as that for positive nursery and retail centre sites shown by David Slawson (this Proceedings), although in both cases there is a downward trend with time.

Relevant to a network perspective is information on whether or not these positive records are thought to have originated in the U.K. This information is needed to fill the knowledge gap about the long-distance and inter-country spread of *P. ramorum* infection (Appiah and others 2004). The origin of the pathogen on the plants can never be stated with certainty - however, where it is suspected that the country that dispatched the plants also dispatched them with an infection of *P. ramorum*, this is notified by the Department for Environment, Food and Rural Affairs (U.K.) to the European Commission, the sending country, the EU member states and EPPO. Although there is variation from month to month, *Figure 2* shows that a substantial proportion of positive findings are thought to originate from abroad. For example, 106 out of 244 positive findings in 2003 (43 percent) in nurseries were on plants of non-U.K. origin. The proportion is similar in 2005 (38 out of 100 findings), in spite of a reduction in the overall number of findings, which suggests that the policy for

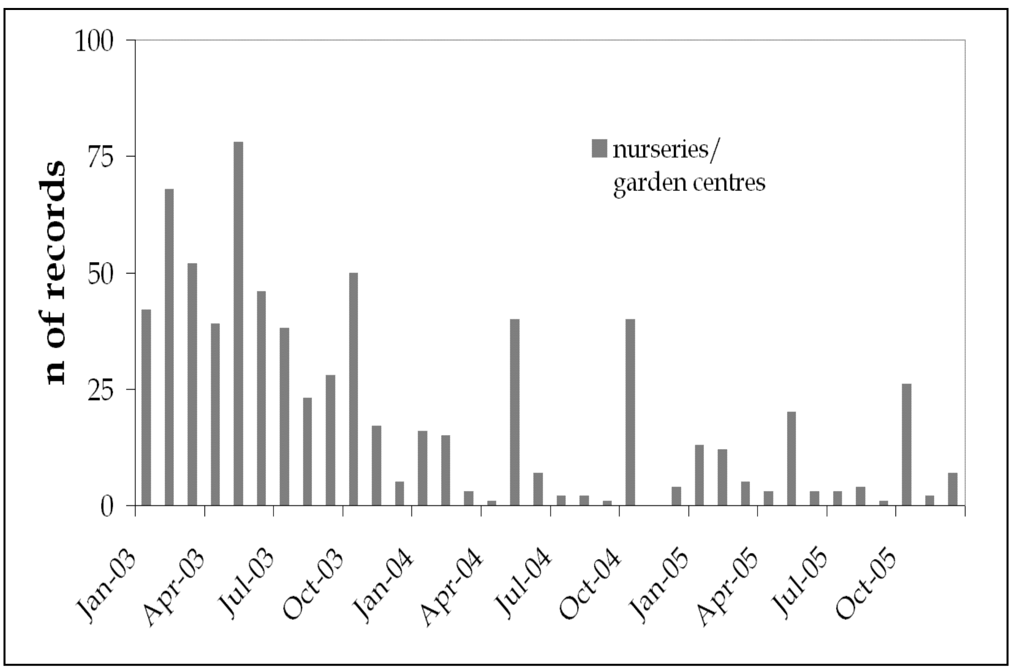

Figure 1—Downward trend of the records positive to *P. ramorum* in nurseries and garden centres (2003-2005) of England and Wales (data source: DEFRA, U.K.).

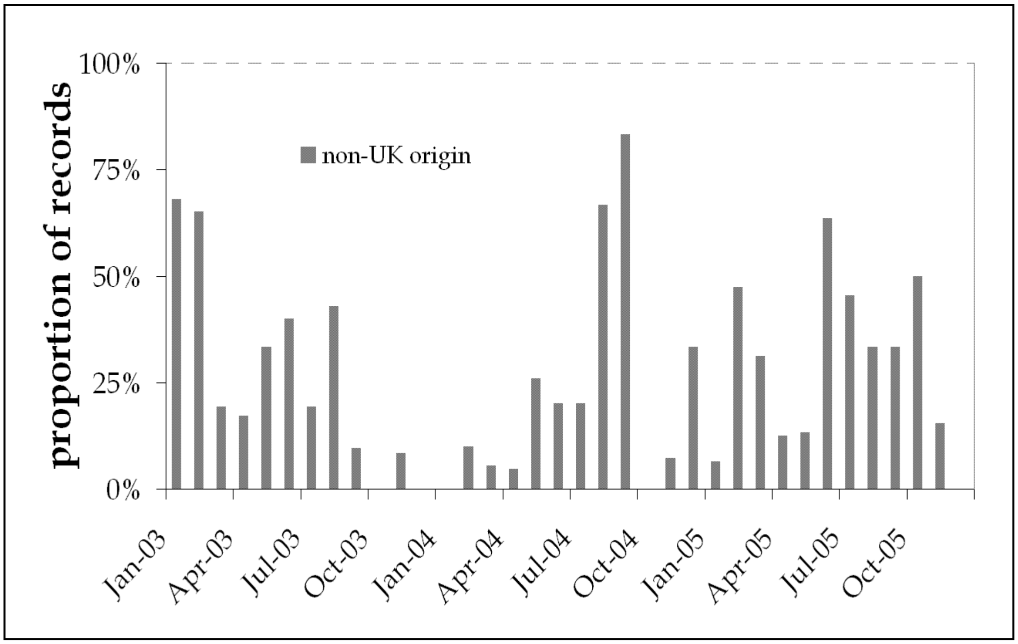

Figure 2—The proportion of *P. ramorum* positive records originating from the U.K. or from other countries (same period and source as fig. 1, but for nurseries only).

dealing with internal disease transmission is working more effectively than the policy for dealing with imports from outside of the U.K. All in all, this is evidence for a small-world scenario in the spread of *P. ramorum*, with local connectivity but also long-distance connections.

Moving from a temporal to a spatial perspective, the distribution of positive findings in woodlands and historic gardens (Fig. 2 in Jeger and others 2007) appears to match the climate suitability of Britain to *P. ramorum* (Appendix 3 in Forestry Commission 2004). Also at a large-scale, disease expression is the result of the interactions amongst host(s), pathogen and environment (Holdenrieder and others 2004, Rizzo and others 2005, Scholthof and others 2007). Since *P. ramorum* hosts (as well as their associations) are fairly widespread, and since the pathogen has been detected in nurseries and garden centres throughout Britain, climate may be the limiting factor restricting disease expression in woodlands and gardens mainly in the West. However, this assumes that the pathogen was first spread by the nursery trade and then moved into woodlands and historic gardens. If instead the pathogen first became established in historic gardens and/or woodlands and then jumped into the nursery trade, the network of plant nurseries has the potential to spread the pathogen also to regions where there are currently no or few outbreaks in woodlands and/or historic gardens. In this perspective the downward trend of *P. ramorum* positive findings in nurseries is to be welcomed. Less encouraging is the increase in the number of positive records in woodlands and historic gardens (Judith Turner, this proceedings).

A network perspective can be applied to the database of *P. ramorum* positive findings also at the level of the different susceptible genera (genera and not species, because for many positive findings only the generic information is available), similar to analyses of mycorrhiza (Southworth and others 2005) and plant-frugivore

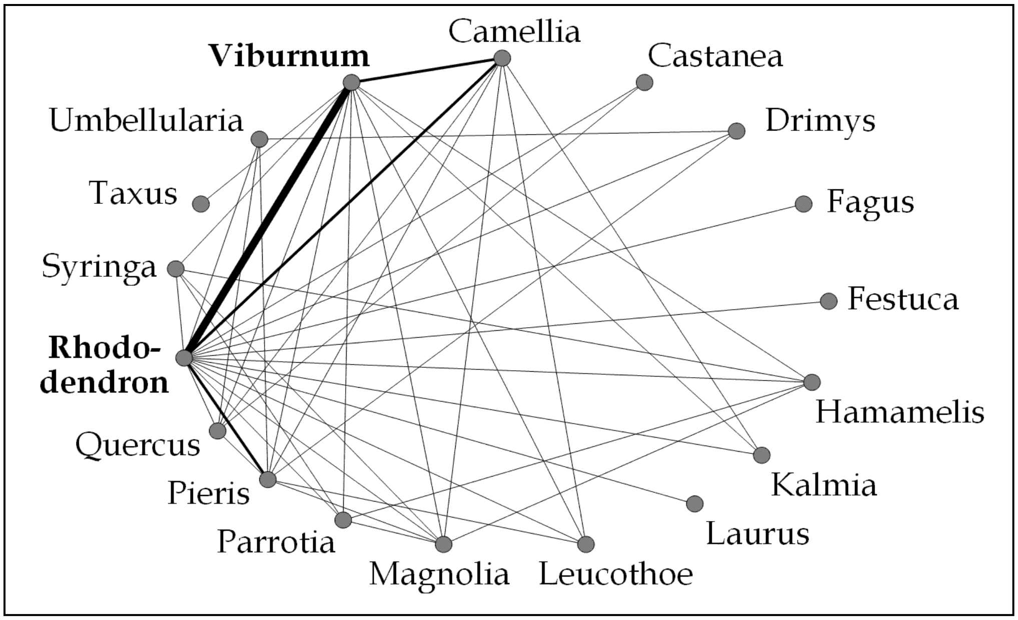

Figure 3—Web of genera susceptible to *P. ramorum*. Two genera are connected if *P. ramorum* was detected on individual plants of these genera at the same location (2003-2005, England and Wales, nursery, garden centers and natural environment, data provided by DEFRA, U.K.). The connection strengths reflect the number of locations connecting the two genera (*Rhododendron-Viburnum*: 55 common locations, *Rhododendron-Camellia*: 17, *Rhododendron-Pieris*: 16, *Viburnum-Camellia*: 10, all other combinations: less than 10 common locations).

networks (Lázaro and others 2005). In this case, two genera are connected if individuals of the genera are found to be infected by the pathogen at the same location (Fig. 3). The resulting network is not homogeneous: some genera are more connected than others. This could be a consequence of *Rhododendron ponticum* being the main host in Britain (68 percent of the positive findings of *P. ramorum* are on *Rhododendron*). This finding supports the current policy focus on high risk species. By targeting locations where super-connected genera occur (in other words *Rhododendron* and *Viburnum*), it is possible to cover most if not the whole of the *P. ramorum* host range.

Also in terms of the number of *P. ramorum* positive records for the different genera, there is evidence for a high heterogeneity of the pathosystem. The frequency distribution of the number of affected genera in terms of the number of positive *P. ramorum* records per affected genus is not log-normal (fig. 4). What one would expect would be a normal distribution, in other words a few genera with a small amount of positive records, a few genera with a large amount of positive records, and most genera with an intermediate number of records. But what we observe is not a normal distribution, as most genera have a few positive records, and only a few genera have many positive records. In fact, this distribution is relatively well fitted by a linear regression in log-log space. This is evidence for the presence of a scale-free property in the database of *P. ramorum* positive findings in England and Wales. Scale-free means that the decrease in the order of magnitude of affected genera with increase in order of magnitude of number of positive records per genus is roughly

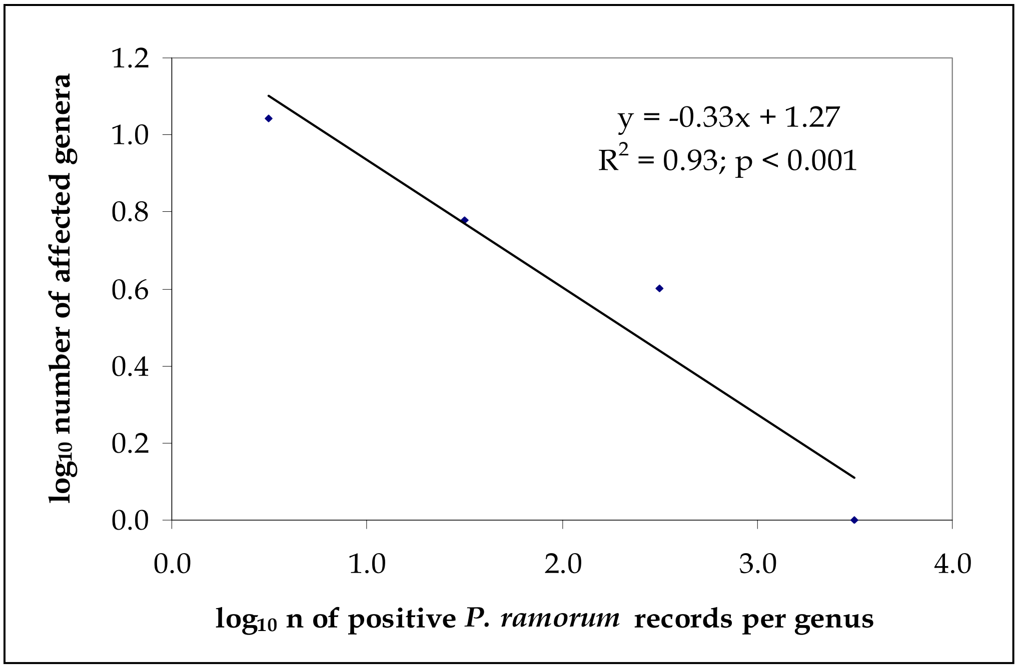

Figure 4—Linear regression of the distribution of the number of affected genera in logarithmic classes of the number of positive *P. ramorum* records (2003–2005, England and Wales, nurseries, garden centres and natural environment, data provided by DEFRA, UK).

similar over the whole range of variation in affected genera and positive records. For a friendly introduction to scale-free networks see for example, Southworth and others (2005). Further work should aim to establish whether the nursery network underlying the spread of *P. ramorum* indeed has a scale-free degree distribution. The degree distribution is the frequency distribution of the number of links of the nurseries involved in the trade of plants susceptible to the pathogen. Unfortunately, this level of information about the structure of the U.K. horticultural trade is not currently available.

The findings that the network involved in the spread of *P. ramorum* in England and Wales is likely to have small-world and scale-free properties is worrying, because such networks have lower epidemic thresholds than local and random networks. However, scale-free networks may improve the chances of preventing further increase in the extent of the regions affected. Provided that long-distance connections and key players in the nursery trade can be identified, by targeting them instead of pursuing complete or random control of nurseries and shipments, it is possible to achieve a more efficient and less costly reduction of the connectivity of the system, as shown by studies of the vulnerability of the North American power grid to random vs. targeted removal of power stations (Albert and others 2004).

Acknowledgments

Many thanks to R. Baker, C. Brasier, A. Brown, S. Denman, O. Holdenrieder, A. Inman, J. Parke, C. Sansford, D. Slawson, J. Turner, J. Webber, and S. Werres for insights and discussions, and to S. Frankel, R. Magarey and C.G. Shaw for helpful comments on a previous version of the draft. This work was funded by the Department for Environment, Food, and Rural Affairs, U.K.

Literature Cited

Albert, R.; Albert, I.; Nakarado, G.L. 2004. Structural vulnerability of the North American power grid. Physical Review E. 69: 025103.

Amaral, L.A.N.; Scala, A.; Barthelemy, M; Stanley, H.E. 2000. Classes of small-world networks. Proceedings of the National Academy of Sciences USA. 97 (21): 11149–11152.

Appiah, A.A.; Jennings, P.; Turner, J.A. 2004. *Phytophthora ramorum*: one pathogen and many diseases, an emerging threat to forest ecosystems and ornamental plant life. Mycologist. 18 (4): 145–150.

Dybiec, B.; Kleczkowski, A.; Gilligan, C.A. 2005. Optimising control of disease spread of on networks. Acta Physica Polonica B. 36 (5): 1509–1526.

Forestry Commission. 2004. Report on the Forestry Commission woodland surveys 2004 to assess the level of incidence of *Phytophthora ramorum* in British woodlands. Forestry Commission, Plant Health Service, Edinburgh, UK.

Gilligan, C.A.; Gubbins, S.; Simons, S.A. 1997. Analysis and fitting of an SIR model with host response to infection load for a plant disease. Philosophical Transactions of the Royal Society London B. 352 (1351): 353–364.

Guimerá, R.; Mossa, S.; Turtschi, A.; Amaral, L.A.N. 2005. The worldwide air transportation network: anomalous centrality, community structure, and cities' global roles. Proceedings of the National Academy of Sciences USA. 102: 7794–7799.

Herrero, M.L.; Toppe, B.; Klemsdal, S.S.; Stensvand, A. 2006. First report of *Phytophthora ramorum* in ornamental plants in Norway. Plant Disease. 90 (11): 1458.

Holdenrieder, O.; Pautasso, M.; Weisberg, P.J.; Londsdale, D. 2004. Tree diseases and landscape processes: the challenge of landscape pathology. Trends in Ecology & Evolution. 19: 446–52.

Hufnagel, L.; Brockmann, D.; Geisel, T. 2004. Forecast and control of epidemics in a globalized world. Proceedings of the National Academy of Sciences USA. 101: 15124–15129.

Jeger, M.J.; Pautasso, M.; Holdenrieder, O.; Shaw, M.W. 2007. Modelling disease spread and control in networks: implications for plant sciences. New Phytologist. 174: 279–297.

Keeling, M.J.; Eames, K.T.D. 2005. Networks and epidemic models. Interface. 2: 295–307.

Lázaro, A.; Mark, S.; Olesen, J.M. 2005. Bird-made fruit orchards in northern Europe: nestedness and network properties. Oikos. 110: 321–329.

May, R.M. 2006. Network structure and the biology of populations. Trends in Ecology & Evolution. 21: 394–399.

Newman, M.E.J. 2003. The structure and function of complex networks. SIAM Review. 45: 167–256.

Parke, J.L.; Linderman, R.G.; Osterbauer, N.K.; Griesbach, J.A. 2004. Detection of *Phytophthora ramorum* blight in Oregon nurseries and completion of Koch's postulates on *Pieris*, *Rhododendron*, *Viburnum* and *Camellia*. Plant Disease. 88 (1): 87–87.

Rizzo, D.M.; Garbelotto, M.; Hansen, E.A. 2005. *Phytophthora ramorum*: integrative research and management of an emerging pathogen in California and Oregon forests. Annual Review of Phytopathology. 43: 309–335.

Scholthof, K.B.G. 2007. The disease triangle: pathogens, the environment and society. Nature Reviews Microbiology. 5 (2): 152–156.

Shirley, M.D.F.; Rushton, S.P. 2005. The impacts of network topology on disease spread. Ecological Complexity. 2: 287–299.

Southworth, D.; He, X.-H.; Swenson, W.; Bledsoe, C.S.; Horwath, W.R. 2005. Application of network theory to potential mycorrhizal networks. Mycorrhiza. 15: 589–595.

Stokstad, E. 2004. Nurseries may have shipped sudden oak death pathogen nationwide. Science. 303: 1959–1959.

Tubajika, K.M.; Bulluck, R.; Shiel, P.J.; Scott, S.E.; Sawyer, A.J. 2006. The occurrence of *Phytophthora ramorum* in nursery stock in California, Oregon, and Washington States. Plant Health Progress. March 2006.

Werres, S.; Marwitz, R.; Man in't Veld, W.A.; de Cock, A.W.A.M.; Bonants, P.J.M.; de Weedt, M.; Themann, K.; Illieva, E.; Baayen, R.P. 2001. *Phytophthora ramorum* sp. nov., a new pathogen on *Rhododendron* and *Viburnum*. Mycological Research 105: 1155–1165.