

AUTHOR'S CORRECTION

Analysis of the *dbpBA* Upstream Regulatory Region Controlled by RpoS in *Borrelia burgdorferi*

Zhiming Ouyang, Shayma Haq, and Michael V. Norgard

Department of Microbiology, University of Texas Southwestern Medical Center, Dallas, Texas 75390

Volume 192, no. 7, p. 1965–1974, 2010. Pages 1973–1974: The References section should appear as shown below.

1. Alverson, J., S. F. Bundle, C. D. Sohaskey, M. C. Lybecker, and D. S. Samuels. 2003. Transcriptional regulation of the *ospAB* and *ospC* promoters from *Borrelia burgdorferi*. *Mol. Microbiol.* **48**:1665–1677.
2. Becker, G., and R. Hengge-Aronis. 2001. What makes an *Escherichia coli* promoter sigma(S) dependent? Role of the $-13/-14$ nucleotide promoter positions and region 2.5 of sigma(S). *Mol. Microbiol.* **39**:1153–1165.
3. Blevins, J. S., K. E. Hagman, and M. V. Norgard. 2008. Assessment of decorin-binding protein A to the infectivity of *Borrelia burgdorferi* in the murine models of needle and tick infection. *BMC Microbiol.* **8**:82.
4. Blevins, J. S., A. T. Revel, A. H. Smith, G. N. Bachlani, and M. V. Norgard. 2007. Adaptation of a luciferase gene reporter and *lac* expression system to *Borrelia burgdorferi*. *Appl. Environ. Microbiol.* **73**:1501–1513.
5. Blevins, J. S., H. Xu, M. He, M. V. Norgard, L. Reitzer, and X. F. Yang. 2009. Rrp2, a sigma54-dependent transcriptional activator of *Borrelia burgdorferi*, activates *rpoS* in an enhancer-independent manner. *J. Bacteriol.* **191**:2902–2905.
6. Boardman, B. K., M. He, Z. Ouyang, H. Xu, X. Pang, and X. F. Yang. 2008. Essential role of the response regulator Rrp2 in the infectious cycle of *Borrelia burgdorferi*. *Infect. Immun.* **76**:3844–3853.
7. Brown, E. L., B. P. Guo, P. O'Neal, and M. Hook. 1999. Adherence of *Borrelia burgdorferi*. Identification of critical lysine residues in DbpA required for decorin binding. *J. Biol. Chem.* **274**:26272–26278.
8. Brown, E. L., R. M. Wooten, B. J. Johnson, R. V. Iozzo, A. Smith, M. C. Dolan, B. P. Guo, J. J. Weis, and M. Hook. 2001. Resistance to Lyme disease in decorin-deficient mice. *J. Clin. Investig.* **107**:845–852.
9. Bunikis, J., L. Noppa, and B. Bergstrom. 1995. Molecular analysis of a 66-kDa protein associated with the outer membrane of Lyme disease *Borrelia*. *FEMS Microbiol. Lett.* **131**:139–145.
10. Burgdorfer, W., A. G. Barbour, S. F. Hayes, J. L. Benach, E. Grunwaldt, and J. P. Davis. 1982. Lyme disease—a tick-borne spirochetosis? *Science* **216**:1317–1319.
11. Burtnick, M. N., J. S. Downey, P. J. Brett, J. A. Boylan, J. G. Frye, T. R. Hoover, and F. C. Gherardini. 2007. Insights into the complex regulation of *rpoS* in *Borrelia burgdorferi*. *Mol. Microbiol.* **65**:277–293.
12. Caimano, M. J., C. H. Eggers, K. R. Hazlett, and J. D. Radolf. 2004. RpoS is not central to the general stress response in *Borrelia burgdorferi* but does control expression of one or more essential virulence determinants. *Infect. Immun.* **72**:6433–6445.
13. Caimano, M. J., R. Iyer, C. H. Eggers, C. Gonzalez, E. A. Morton, M. A. Gilbert, I. Schwartz, and J. D. Radolf. 2007. Analysis of the RpoS regulon in *Borrelia burgdorferi* in response to mammalian host signals provides insight into RpoS function during the enzootic cycle. *Mol. Microbiol.* **65**:1193–1217.
14. Coburn, J. 2001. Adhesion mechanisms of the Lyme disease spirochete, *Borrelia burgdorferi*. *Curr. Drug Targets Infect. Disord.* **1**:171–179.
15. Coburn, J., W. Chege, L. Magoun, S. C. Bodary, and J. M. Leong. 1999. Characterization of a candidate *Borrelia burgdorferi* beta3-chain integrin ligand identified using a phage display library. *Mol. Microbiol.* **34**:926–940.
16. Coburn, J., J. R. Fischer, and J. M. Leong. 2005. Solving a sticky problem: new genetic approaches to host cell adhesion by the Lyme disease spirochete. *Mol. Microbiol.* **57**:1182–1195.
17. de Silva, A. M., K. R. Tyson, and U. Pal. 2009. Molecular characterization of the tick-*Borrelia* interface. *Front. Biosci.* **14**:3051–3063.
18. Eggers, C. H., M. J. Caimano, and J. D. Radolf. 2004. Analysis of promoter elements involved in the transcriptional initiation of RpoS-dependent *Borrelia burgdorferi* genes. *J. Bacteriol.* **186**:7390–7402.
19. Frank, K. L., S. F. Bundle, M. E. Kresge, C. H. Eggers, and D. S. Samuels. 2003. *adaA* confers streptomycin resistance in *Borrelia burgdorferi*. *J. Bacteriol.* **185**:6723–6727.
20. Fraser, C. M., S. Casjens, W. M. Huang, G. G. Sutton, R. Clayton, R. Lathigra, O. White, K. A. Ketchum, R. Dodson, E. K. Hickey, M. Gwinn, B. Dougherty, J. F. Tomb, R. D. Fleischmann, D. Richardson, J. Peterson, A. R. Kerlavage, J. Quackenbush, S. Salzberg, M. Hanson, R. van Vugt, N. Palmer, M. D. Adams, J. Gocayne, J. Weidman, T. Utterback, L. Wathley, L. McDonald, P. Artiach, C. Bowman, S. Garland, C. Fuji, M. D. Cotton, K. Horst, K. Roberts, B. Hatch, H. O. Smith, and J. C. Venter. 1997. Genomic sequence of a Lyme disease spirochete, *Borrelia burgdorferi*. *Nature* **390**:580–586.
21. Grimm, D., K. Tilly, R. Byram, P. E. Stewart, J. G. Krum, D. M. Bueschel, T. G. Schwan, P. F. Policastro, A. F. Elias, and P. A. Rosa. 2004. Outer-surface protein C of the Lyme disease spirochete: a protein induced in ticks for infection of mammals. *Proc. Natl. Acad. Sci. USA* **101**:3142–3147.
22. Guo, B. P., E. L. Brown, D. W. Dorward, L. C. Rosenberg, and M. Hook. 1998. Decorin-binding adhesins from *Borrelia burgdorferi*. *Mol. Microbiol.* **30**:711–723.
23. Guo, B. P., S. J. Norris, L. C. Rosenberg, and M. Hook. 1995. Adherence of *Borrelia burgdorferi* to the proteoglycan decorin. *Infect. Immun.* **63**:3467–3472.
24. Hagman, K. E., P. Lahdenne, T. G. Popova, S. F. Porcella, D. R. Akins, J. D. Radolf, and M. V. Norgard. 1998. Decorin-binding protein of *Borrelia burgdorferi* is encoded within a two-gene operon and is protective in the murine model of Lyme borreliosis. *Infect. Immun.* **66**:2674–2683.
25. Hagman, K. E., X. Yang, S. K. Wikel, G. B. Schoeler, M. J. Caimano, J. D. Radolf, and M. V. Norgard. 2000. Decorin-binding protein A (DbpA) of *Borrelia burgdorferi* is not protective when immunized mice are challenged via tick infestation and correlates with the lack of DbpA expression by *B. burgdorferi* in ticks. *Infect. Immun.* **68**:4759–4764.
26. Hozdic, E., S. Feng, K. J. Freet, D. L. Borjesson, and S. W. Barthold. 2002. *Borrelia burgdorferi* population kinetics and selected gene expression at the host-vector interface. *Infect. Immun.* **70**:3382–3388.
27. Hübner, A., X. Yang, D. M. Nolen, T. G. Popova, F. C. Cabello, and M. V. Norgard. 2001. Expression of *Borrelia burgdorferi* OspC and DbpA is controlled by a RpoN-RpoS regulatory pathway. *Proc. Natl. Acad. Sci. USA* **98**:12724–12729.
28. Hyde, J. A., J. P. Trzeciakowski, and J. T. Skare. 2007. *Borrelia burgdorferi* alters its gene expression and antigenic profile in response to CO₂ levels. *J. Bacteriol.* **189**:437–445.
29. Liang, F. T., M. B. Jacobs, L. C. Bowers, and M. T. Philipp. 2002. An immune evasion mechanism for spirochetal persistence in Lyme borreliosis. *J. Exp. Med.* **195**:415–422.
30. Liang, F. T., J. Yan, M. L. Mbow, S. L. Sviat, R. D. Gilmore, M. Mamula, and E. Fikrig. 2004. *Borrelia burgdorferi* changes its surface antigenic expression in response to host immune responses. *Infect. Immun.* **72**:5759–5767.
31. Lybecker, M. C., and D. S. Samuels. 2007. Temperature-induced regulation of RpoS by a small RNA in *Borrelia burgdorferi*. *Mol. Microbiol.* **64**:1075–1089.
32. Neelakanta, G., X. Li, U. Pal, X. Liu, D. S. Beck, K. DePonte, D. Fish, F. S. Kantor, and E. Fikrig. 2007. Outer surface protein B is critical for *Borrelia burgdorferi* adherence and survival within *Ixodes* ticks. *PLoS Pathog.* **3**:e33.
33. Ouyang, Z., J. S. Blevins, and M. V. Norgard. 2008. Transcriptional interplay among the regulators Rrp2, RpoN and RpoS in *Borrelia burgdorferi*. *Microbiology* **154**:2641–2658.
34. Pal, U., A. M. de Silva, R. R. Montgomery, D. Fish, J. Anguita, J. F. Anderson, Y. Lobet, and E. Fikrig. 2000. Attachment of *Borrelia burgdorferi* within *Ixodes scapularis* mediated by outer surface protein A. *J. Clin. Investig.* **106**:561–569.
35. Pal, U., X. Li, T. Wang, R. R. Montgomery, N. Ramamoorthi, A. M. Desilva, F. Bao, X. Yang, M. Pypaert, D. Pradhan, F. S. Kantor, S. Telford, J. F. Anderson, and E. Fikrig. 2004. TROSPA, an *Ixodes scapularis* receptor for *Borrelia burgdorferi*. *Cell* **119**:457–468.
36. Pal, U., X. Yang, M. Chen, L. K. Bockenstedt, J. F. Anderson, R. A. Flavell, M. V. Norgard, and E. Fikrig. 2004. OspC facilitates *Borrelia burgdorferi* invasion of *Ixodes scapularis* salivary glands. *J. Clin. Investig.* **113**:220–230.

37. Parveen, N., and J. M. Leong. 2000. Identification of a candidate glycosaminoglycan-binding adhesin of the Lyme disease spirochete *Borrelia burgdorferi*. *Mol. Microbiol.* **35**:1220–1234.
38. Pikas, D. S., E. L. Brown, S. Gurusiddappa, L. Y. Lee, Y. Xu, and M. Hook. 2003. Decorin-binding sites in the adhesin DbpA from *Borrelia burgdorferi*: a synthetic peptide approach. *J. Biol. Chem.* **278**:30920–30926.
39. Pollack, R. J., S. R. Telford III, and A. Spielman. 1993. Standardization of medium for culturing Lyme disease spirochetes. *J. Clin. Microbiol.* **31**:1251–1255.
40. Probert, W. S., and B. J. Johnson. 1998. Identification of a 47 kDa fibronectin-binding protein expressed by *Borrelia burgdorferi* isolate B31. *Mol. Microbiol.* **30**:1003–1015.
41. Revel, A. T., J. S. Blevins, C. Almazan, L. Neil, K. M. Kocan, J. de la Fuente, K. E. Hagman, and M. V. Norgard. 2005. *bptA* (*bbe16*) is essential for the persistence of the Lyme disease spirochete, *Borrelia burgdorferi*, in its natural tick vector. *Proc. Natl. Acad. Sci. USA* **102**:6972–6977.
42. Rosa, P. A., K. Tilly, and P. E. Stewart. 2005. The burgeoning molecular genetics of the Lyme disease spirochaete. *Nat. Rev. Microbiol.* **3**:129–143.
43. Samuels, D. S. 1995. Electrotransformation of the spirochete *Borrelia burgdorferi*. *Methods Mol. Biol.* **47**:253–259.
44. Schwan, T. G., J. Piesman, W. T. Golde, M. C. Dolan, and P. A. Rosa. 1995. Induction of an outer surface protein on *Borrelia burgdorferi* during tick feeding. *Proc. Natl. Acad. Sci. USA* **92**:2909–2913.
45. Seshu, J., J. A. Boylan, F. C. Gherardini, and J. T. Skare. 2004. Dissolved oxygen levels alter gene expression and antigen profiles in *Borrelia burgdorferi*. *Infect. Immun.* **72**:1580–1586.
46. Shi, Y., Q. Xu, K. McShan, and F. T. Liang. 2008. Both decorin-binding proteins A and B are critical for overall virulence of *Borrelia burgdorferi*. *Infect. Immun.* **76**:1239–1246.
47. Shi, Y., Q. Xu, S. V. Seemanapli, K. McShan, and F. T. Liang. 2008. Common and unique contributions of decorin-binding proteins A and B to the overall virulence of *Borrelia burgdorferi*. *PLoS One* **3**:e3340.
48. Smith, A. H., J. S. Blevins, G. N. Bachlani, X. F. Yang, and M. V. Norgard. 2007. Evidence that RpoS (σ 54) in *Borrelia burgdorferi* is controlled directly by RpoN (σ 54/ σ 70). *J. Bacteriol.* **189**:2139–2144.
49. Steere, A. C., J. Coburn, and L. Glickstein. 2004. The emergence of Lyme disease. *J. Clin. Investig.* **113**:1093–1101.
50. Steere, A. C., R. L. Grodzicki, A. N. Kornblatt, J. E. Craft, A. G. Barbour, W. Burgdorfer, G. P. Schmid, E. Johnson, and S. E. Malawista. 1983. The spirochetal etiology of Lyme disease. *N. Engl. J. Med.* **308**:733–740.
51. Stewart, P. E., R. Thalken, J. L. Bono, and P. Rosa. 2001. Isolation of a circular plasmid region sufficient for autonomous replication and transformation of infectious *Borrelia burgdorferi*. *Mol. Microbiol.* **39**:714–721.
52. Tokarz, R., J. M. Anderton, L. I. Katona, and J. L. Benach. 2004. Combined effects of blood and temperature shift on *Borrelia burgdorferi* gene expression as determined by whole genome DNA array. *Infect. Immun.* **72**:5419–5432.
53. Typas, A., G. Becker, and R. Hengge. 2007. The molecular basis of selective promoter activation by the σ 54 subunit of RNA polymerase. *Mol. Microbiol.* **63**:1296–1306.
54. Weening, E. H., N. Parveen, J. P. Trzeciakowski, J. M. Leong, M. Hook, and J. T. Skare. 2008. *Borrelia burgdorferi* lacking DbpA exhibits an early survival defect during experimental infection. *Infect. Immun.* **76**:5694–5705.
55. Xu, Q., K. McShan, and F. T. Liang. 2007. Identification of an *ospC* operator critical for immune evasion of *Borrelia burgdorferi*. *Mol. Microbiol.* **64**:220–231.
56. Yang, X., M. S. Goldberg, T. G. Popova, G. B. Schoeler, S. K. Wikel, K. E. Hagman, and M. V. Norgard. 2000. Interdependence of environmental factors influencing reciprocal patterns of gene expression in virulent *Borrelia burgdorferi*. *Mol. Microbiol.* **37**:1470–1479.
57. Yang, X., T. G. Popova, K. E. Hagman, S. K. Wikel, G. B. Schoeler, M. J. Caimano, J. D. Radolf, and M. V. Norgard. 1999. Identification, characterization, and expression of three new members of the *Borrelia burgdorferi* Mlp (2.9) lipoprotein gene family. *Infect. Immun.* **67**:6008–6018.
58. Yang, X. F., S. M. Alani, and M. V. Norgard. 2003. The response regulator Rrp2 is essential for the expression of major membrane lipoproteins in *Borrelia burgdorferi*. *Proc. Natl. Acad. Sci. USA* **100**:11001–11006.
59. Yang, X. F., M. C. Lybecker, U. Pal, S. M. Alani, J. Blevins, A. T. Revel, D. S. Samuels, and M. V. Norgard. 2005. Analysis of the *ospC* regulatory element controlled by the RpoN-RpoS regulatory pathway in *Borrelia burgdorferi*. *J. Bacteriol.* **187**:4822–4829.